TAXONOMY OF LANTANA SECT. LANTANA (VERBENACEAE): I. CORRECT APPLICATION OF LANTANA CAMARA AND ASSOCIATED NAMES

Roger W. Sanders

Botanical Research Institute of Texas 509 Pecan Street Fort Worth, Texas 76102-4060, U.S.A. rsanders@brit.org

ABSTRACT

The previous lectotypification of *Lantana camara* L. is evaluated by examination of characters of the lectotype, review of other original material, and documentation of current usage of the name. The current usage is analyzed by surveying pertinent literature and by sampling specimens for annotations between 1753 and the present in relation to critical characters of those specimens. Current usage of *L. camara* includes a widely cultivated and naturalized cultigen species of hybrid origin that is taxonomically distinct from *L. camara*. To determine the correct name of the cultigen, all names in *Lantana* sect. *Lantana* are reviewed, typified if necessary and possible, and taxonomically disposed. No available name applies to the cultigen, which is newly described as *Lantana strigocamara* R.W. Sanders. Origin of the named hybrids in the *L. camara* complex is hypothesized. Two new combinations are made, *Lantana camara* subsp. *aculeata* (L.) R.W. Sanders and *Lantana nivea* Vent. subsp. *mutabilis* (W.J. Hook.) R.W. Sanders. Nineteen lectotypifications and seven epitypifications are made.

RESUMEN

La lectotipificación previa de *Lantana camara* L. se evalúa mediante examen de los caracteres del lectotipo, revisión de otro material original, y documentación del uso actual del nombre. El uso actual se analizó revisando la bibliografía adecuada y por muestreo de especimenes entre 1753 y el presente por comentarios en relación a caracteres críticos de esos especimenes. El uso actual de *L. camara* incluye una especie ampliamente cultivada y naturalizada de origen híbrido que es taxonómicamente diferente de *L. camara*. Para determinar el nombre correcto de la planta cultivada se revisaron todos los nombre de *Lantana* sect. *Lantana*, se tipificaron cuando fue necesario y posible, y taxonómicamente decidido. No hay nombres disponibles para la planta cultivada, que se describe como *Lantana strigocamara* R.W. Sanders. Se hace una hipótesis del origen de los híbridos nombrados en el complejo *L. camara*. Se hacen dos combinaciones nuevas, *Lantana camara* subsp. *aculeata* (L.) R.W. Sanders y *Lantana nivea* Vent. subsp. *mutabilis* (W.J. Hook.) R.W. Sanders. Se realizan diez y nueve lectotipificaciones y siete epitipificaciones.

Plants that have gone under the Linnaean name *Lantana camara* L. are well known, not only as hardy summer ornamentals worldwide but also as naturalized weeds having devastating economic impact in humid tropical areas of the Old World (Wolfson & Solomons 1964; Howard 1970; Stirton 1977; Swarbrick et al. 1995; Day et al. 2003). The systematics of these cultivated and naturalized plants is not well understood, even though considerable effort has been made to elucidate their biological control (Day et al. 2003). This confusion arises in

part from the convoluted history of exploration, cultivation, hybridization, and artificial selection that began at least 60 years before the publication of Linnaeus' *Species Plantarum* (1753). Records that have been compiled (Howard 1969; Stirton 1977) suggest that, during the eighteenth century, fanciers hybridized different wild species and infraspecific taxa of *Lantana* L. sect. *Lantana* from Mexico, the West Indies, and Brazil. As shown in this paper, the early validly published names were based on garden-grown material (almost entirely so until 1817 and commonly so into the 1850s), much of which consisted of hybrid combinations.

As herbarium specimens of wild-collected species of sect. *Lantana* became available after the early 1800s, many of the available, poorly distinguished names were frequently misapplied to them. Adding to this confusion was the introduction of cultivated hybrids into neotropical regions where indigenous taxa occur. Due to the propensity of lantanas to undergo polyploidy and the partial fertility of odd polyploid levels (Natarajan & Ahuja 1957; Khoshoo & Mahal 1967; Spies 1983, 1984; Spies & Stirton 1982a, b, c; Sanders 1987a, b), even more complex hybrids formed between indigenous taxa and the escaped hybrid cultigens (Sanders 1987a, b, c, 1989a). Thus, the limits of natural variation have been obscured, hampering the ability of taxonomists to develop effective classifications for the group.

Schauer (1847), Briquet (1895), and Troncoso (1974) developed current sectional concepts. Species of *Lantana* sect. *Lantana* (=sect. *Camara* Cham.) are characterized by predominantly narrow floral bracts that are somewhat inconspicuous among the tubular corolla bases, by usually yellow or orange pigmented corollas (white-flowered populations known in several species [unpubl. observ.]; see also discussion below concerning purplish pigments in the section), and by blackish drupes. Each drupe contains a characteristically inflated compound endocarp that resembles a horse's skull in which the seed chambers are in the position of the eye sockets. Some of the species of the other major section, *Lantana* sect. *Callioreas* Cham., might be confused with those of sect. *Lantana*. Generally, species of sect. *Callioreas* are described as involucrate, usually having ovate to reniform conspicuously imbricate floral bracts and purplish corollas. However, fruits are needed to insure correct sectional placement—drupes are usually white or purplish and endocarps are subglobose, bilobed (seed chambers fill each hemisphere), noninflated, and reticulately ornamented.

Schauer (1847) published the only worldwide revision of *Lantana* in De Candolle's *Prodromus*. All more recent work has been limited to regional and garden floras. The foremost student of Verbenaceae in the twentieth century, Harold N. Moldenke, never produced a revision of *Lantana*, but he did describe a number of new species and infraspecific taxa. Horticulturalists, ecologists, and some floristic taxonomists have effectively submerged much of *Lantana* sect. *Lantana* into *L. camara*, treating this wide spectrum of variation as a single

species, (e.g., Kuntze 1891; Troncoso 1965, 1974; Bailey Hortorium 1976; Schemske 1976, Huxley et al. 1992; Cullen et al. 2000).

Sanders (1987a, b, c, 1989a, b) undertook a study of the variation of wild and naturalized populations of Lantana sect. Lantana in Florida and parts of the West Indies. By correlating chromosome numbers and meiotic behavior with morphology, he was able to distinguish the natural (often diploid) wild taxa from the naturalized and spontaneous hybrids and to develop morphological taxonomic criteria. Sanders found that plant architecture, leaf and bract size and shape, indument features, inflorescence/infructescence development and size, fruiting bract persistence, and floral pigment classes and dosage effects correlate well with cytology, geographic distributions, and species delimitations. On the other hand, he argued that development of prickles and specific corolla colors, characters relied upon by many other authors, vary too widely within and among taxa to be effective criteria, a conclusion recently supported by molecular studies (Scott et al. 1997; Day et al. 2003). Further support comes from the work of Isidro Méndez S. of Cuba who took up the study of Cuban and West Indian Verbenaceae (1992, 1993, 2002). Méndez explicitly accepted the taxonomic criteria proposed by Sanders for Lantana sect. Lantana.

The natural taxa of sect. Lantana fall into three separate phenetic groups (to be validated in a subsequent paper; cladistic status not yet determined) on the basis of trichome structure on the abaxial surface of the leaf blades, as well as shape, adaxial luster, and venation of the leaf blades. The "pilose-morph" species (Pilose Group, Fig. 1) are characterized by soft, filiform, spreading (erect or curly) hairs usually densely disposed on all veins and intervening tissue. Most of these have leaf blades that are broadly ovate to narrowly deltate, rounded to cordate at the base and acuminate to obtuse at the apex, dull above (epidermis poorly reflective), and more or less pinninerved. The "strigose-morph" species (Strigose Group, Fig. 2) have the abaxial hairs developed as conspicuous strigae, i.e., the hairs are stout, conical, antrorsely geniculate, and are scattered and restricted to the midrib, and secondary, tertiary, and sometimes higher order veins, but not to the intervening tissue. Leaf blades are usually ovate-elliptic, often tapering at base and apex, lustrous above, and more or less triplinerved. The "setose-morph" species (Setose Group, Fig. 3) abaxially bear well-separated, long, flexible to subrigid, spreading, setiform trichomes that are more or less restricted to the midrib and secondary and tertiary veins. Otherwise they are like the pilose-morph species. Thus, even though all three groups have adaxial strigae, the Stigose Group is the only one with strigae on both surfaces.

Despite Méndez's (2002) acceptance of Sanders' criteria, he disagreed with Sanders over the application of the name *L. camara*. Because *L. camara* is the proposed type of the genus (Jarvis 1992; Jarvis et al. 1993) and one of the two oldest names in the secton, the correct application of most other names in the

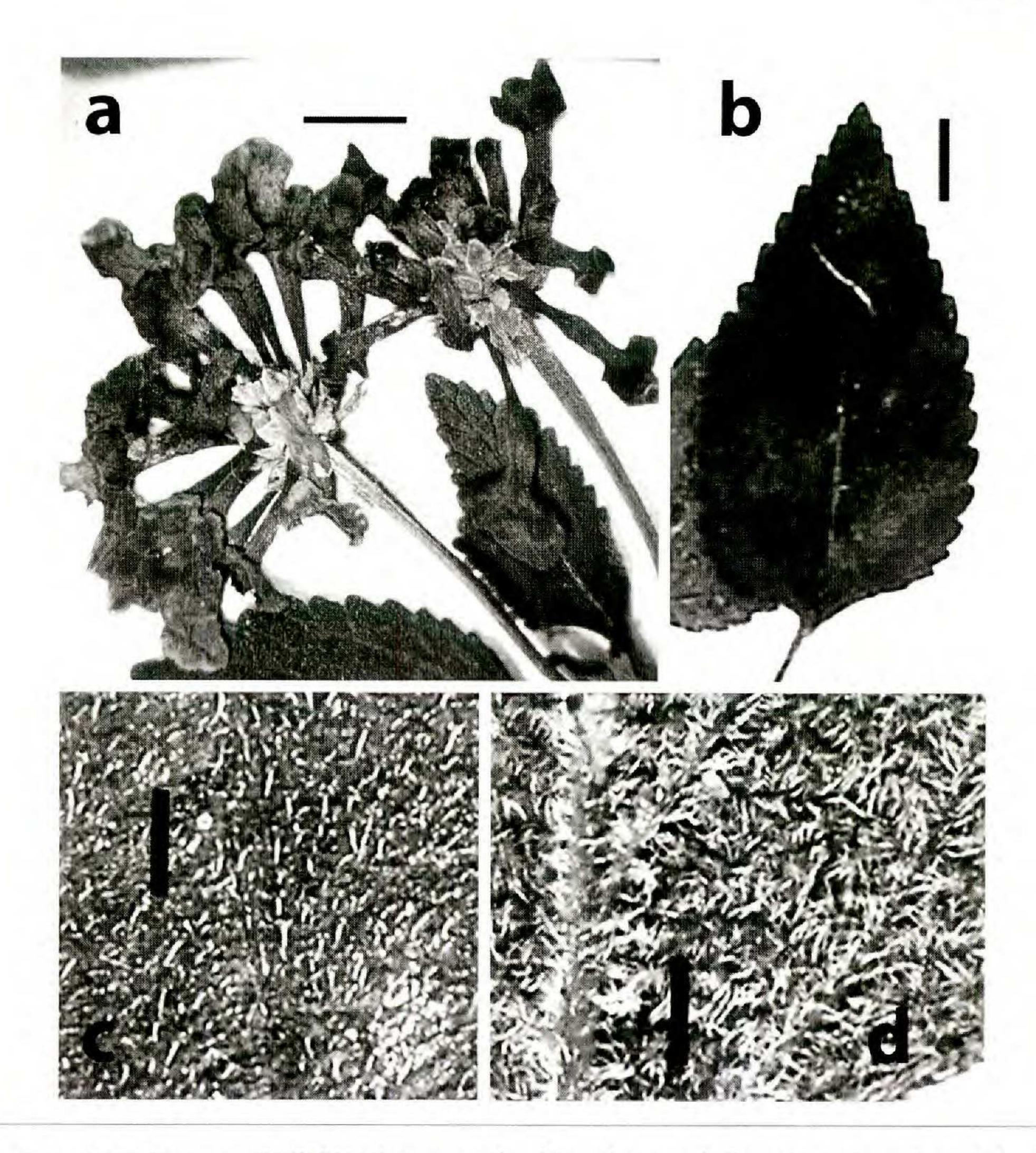


Fig. 1. Lantana camara, lectotype (LINN 783.4), representing Pilose Group. **a.** inflorescence. **b.** representative leaf blade. **c.** adaxial leaf surface. **d.** abaxial leaf surface. Scale bars: a & b = 5 mm; c & d = 1 mm.

section hinge upon the correct application of *L. camara*. Asserting that Sanders had committed two errors, Méndez stated:

Sanders (1989[a]) attributed this binomial [*L. camara*] to a phenotype very different from prevailing opinion among the authors later to Linnaeus and not in agreement with the lectotype selected by Moldenke & Moldenke (1983).

However, until the present study, analysis of the lectotype and subsequent application of the name have not been straightforward. The critical characters were not visible on the lectotype since all of its leaves were mounted adaxial side up. Sanders (unpubl.) was not able to determine whether the lectotype matched the pilose-morph or the strigose-morph plants, especially given the quality of the microfiche and xerographic images available at the time. However, because H. N. Moldenke had selected the type, Sanders (unpubl.) relied primarily on the numerous annotations of Dr. Moldenke (Table 1, App. B, see also Moldenke 1980a) to develop a concept of the species and apply the name. Sanders' concept was further reinforced by annotations of C.D. Adams, and the

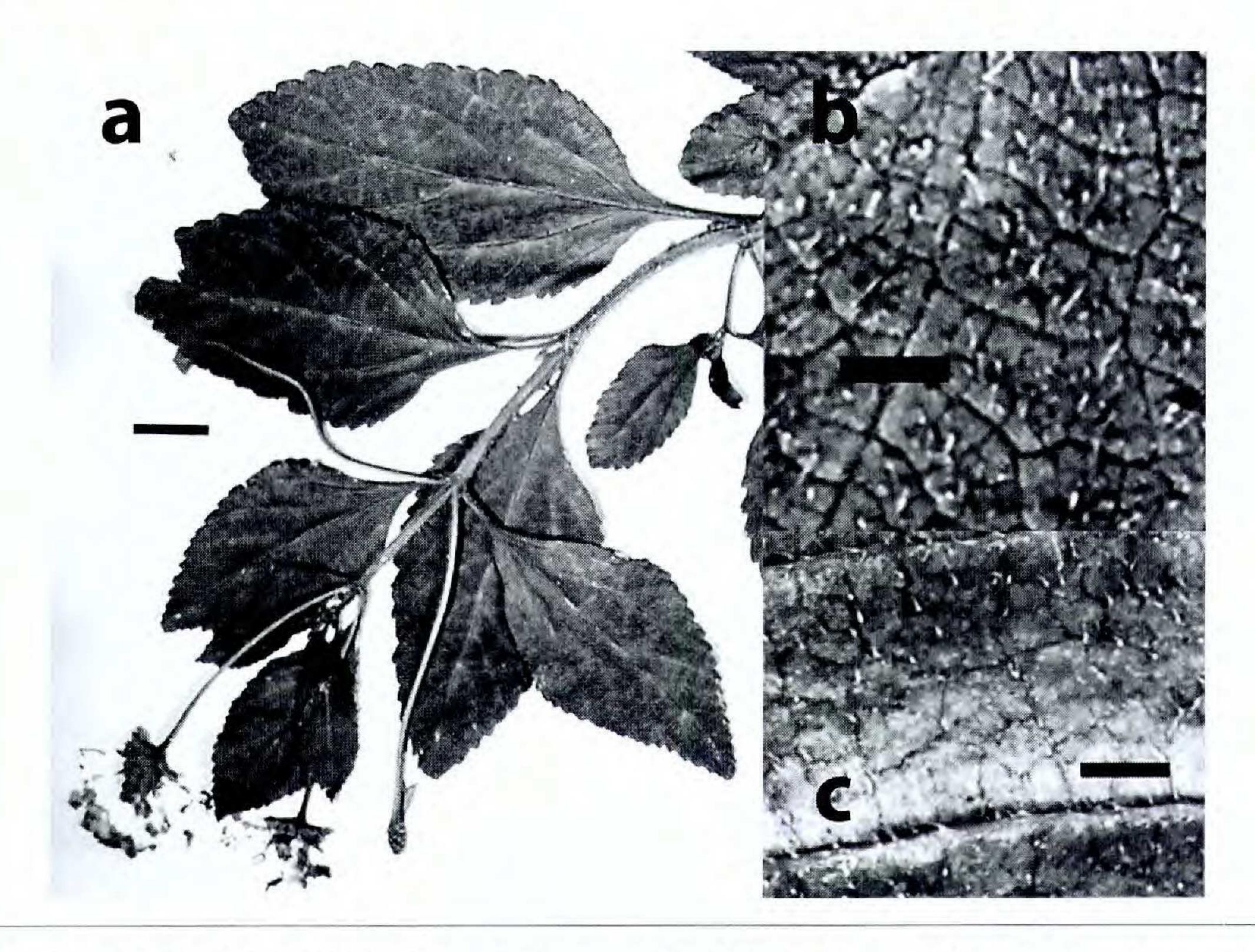


Fig. 2. Lantana scabrida, lectotype (Solander s.n?., BM), representing Strigose Group. **a.** inflorescence and representative leaves. **b.** adaxial leaf surface. **c.** abaxial leaf surface. Scale bars: a = 1 cm; b & c = 1 mm.

treatments of Lantana in The Flowering Plants of Jamaica (Adams 1972) and A Flora of Tropical Florida (Long & Lakela 1971), as well as on identified cultivated material received under that name from the U.S. National Arboretum, Longwood Gardens, and reputable commercial nurseries. In all cases, the plants were characterized by leaves dominated by strigose-morph hairs, cordate-ovate blades, and dull upper surfaces¹ (here subsequently called the "Strigose-Cordate-Dull-" or "SCD cultigen"; Fig. 4). In the West Indies, some wild-collected specimens bear codominant mixtures of both hair morphs. However, cytological study confirmed these to be hybrids between the SCD cultigen and native taxa of the Pilose Group (Sanders 1987b). Thus, Sanders concluded that the lectotype had the strigose-morph hairs, and he applied the name L. camara specifically to the SCD cultigen. Many of the described species in the Pilose Group (including L. horrida, L. tiliifolia, and L. arida) he lumped into a single species and applied the name L. urticifolia Mill.

Méndez appears to have studied more recent, higher quality images in connection with a project to lectotypify Linnaean species of Verbenaceae of the West Indies in collaboration with Steve Cafferty of the Linnaean Typification Project (Méndez & Cafferty 2001). Although he, too, was unable to see the abaxial surfaces, he concluded on other grounds that the lectotype matched the pilose-

¹Adams included in his concept of *L. camara* the SCD cultigen and *L. scabrida*. The few specimens of *L. scabrida* that I studied and bear his annotation as *L. camara* actually have lustrous upper leaf surfaces.



Fig. 3. Lantana hirsuta (Hinton 20499, TEX), representing Setose Group. **a.** inflorescence. **b.** adaxial leaf surface. **c.** abaxial leaf surface. Scale bars: a = 5 mm; b & c = 1 mm.

morph, not the strigose-morph plants. He applied the name *L. camara* to the taxon to which Sanders applied the name *L. urticifolia*.

If Méndez's two assertions merit redress, then another, later-published name should be applied to the SCD cultigen that Moldenke, Adams, and Sanders called *Lantana camara*. Of course, current usage, regardless of usage by authors of the early post-Linnaean period, must be established. If current usage of *L. camara* has clearly replaced the Linnaean concept with the concept of the SCD cultigen, then conservation of the nomenclatural type could serve as an alternative solution.

Therefore the purpose here is to 1) evaluate the lectotypification by reviewing its publication, by clarifying the characters of the lectotype, by understanding current usage of *L. camara*, and by determining any variance between the type and current usage; 2) affirm the correct application of that name, 3) if necessary, determine which other name is to be applied to the SCD cultigen, and 4) dispose of all other names, known to me, that are applicable to the complex.

Typification of Lantana camara

Moldenke and Moldenke (1983) effectively lectotypified *Lantana camara* by citing LINN 783.4 as "type" (ICBN, Art. 7.11, Greuter et al. 2000). This lectotypification was accepted by Sanders (1989b) and Méndez (2002). In March, 2004, I visited BM, and Dr. Charles Jarvis, long-time participant in the Linnaean Typification Project, consented to break the lower stem to permit study of the abaxial surface of the lowest two leaves (Fig. 1). The type, indeed, is of the pilose-morph and is verified by leaf shape and inflorescence structure as an element of the naturally occurring species distributed from the Bahamas and Greater Antilles, through Mexico south to northwestern South America. Thus of Méndez's two assertions, the one that "Sanders (1989) attributed this binomial to a phenotype...not in agreement with the lectotype selected by Moldenke and Moldenke (1983)" is correct.

Table 1. Data documenting history of annotation by H.N. Moldenke and other taxonomists familiar with the classification of Lantana. "v. moritz" indicates plants annotated as L. camara var. moritziana. See text for further discussion.

Years	Authorities	N	Pilose	%	Mixed	%	Strigose	%	Setose	%
1981–2005	Moldenke (incl. v. moritz)	62	15	24%	20	32%	27	44%	0	0%
	Moldenke (excl. v. moritz)	47	0	0%	20	43%	27	57%	0	0%
	Other	45	0	0%	25	56%	20	44%	0	0%
	All (incl. v. moritz)	107	15	14%	45	42%	47	44%	0	0%
	All (excl. v. moritz)	92	0	0%	45	49%	47	51%	0	0%
1956-1980	Moldenke (incl. v. moritz)	153	13	8%	56	37%	83	54%	1	1%
	Moldenke (excl. v. moritz)	141	1	1%	56	40%	83	59%	1	1%
	Other	60	0	0%	41	68%	19	32%	0	0%
	All (incl. v. moritz)	213	13	6%	97	46%	102	48%	1	0%
	All (excl. v. moritz)	201	1	0%	97	48%	102	51%	1	0%
1931-1955	Moldenke	16	2	13%	6	38%	7	44%	1	6%
	Other	1	0	0%	0	0%	1	100%	0	0%
	All	17	2	12%	6	35%	8	47%	1	6%
1906-1930	All	16	0	0%	10	62%	6	38%	0	0%
1881-1905	All	4	0	0%	3	75%	1	25%	0	0%
1856-1880	All	2	0	0%	0	0%	2	100%	0	0%
1831-1855	All	3	1	33%	1	33%	1	33%	0	0%
1753-1830	All	15	10	67%	2	13%		7%	2	139

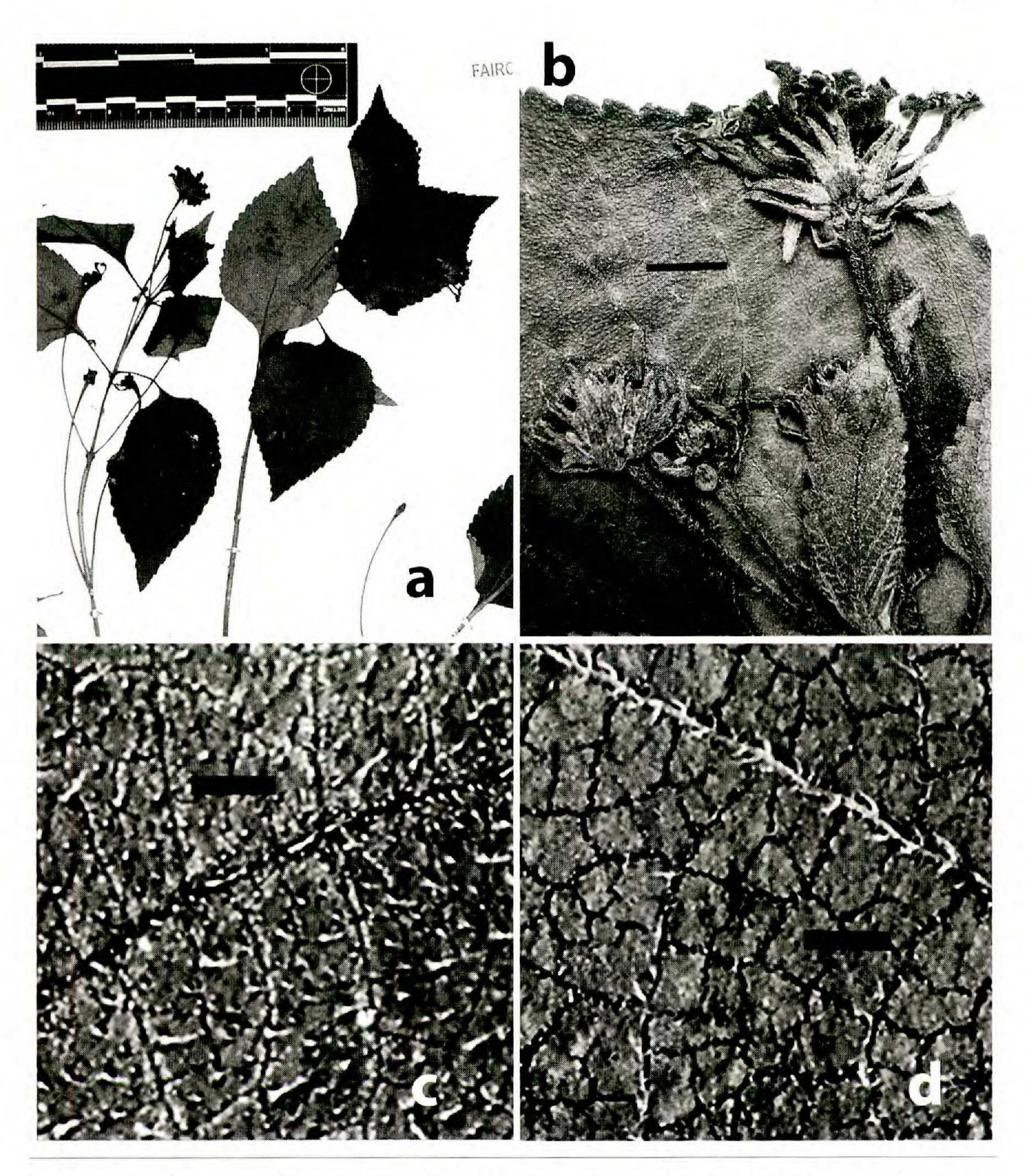


Fig. 4. Lantana strigocamara, holotype (Sanders 1450, FTG). **a.** inflorescences and representative leaves. **b.** inflorescence. **c.** adaxial leaf surface. **d.** abaxial leaf surface. Scale bars: b = 5 mm; c & d = 1 mm.

Development of current usage

Linnaeus' concept of *L. camara* was developed from an array of cultivated and horticulturally selected plants. The synonyms and illustrations that he cited in the protologue are based on vouchers that are primarily elements of the Pilose Group. All Hortus Cliffortianus (1737) specimens are either the same species as LINN 783.4 (319 Lantana 1-B!, Linn. Herb. specimen at S [a cut-down Herb. Cliff. specimen, *C. Jarvis*, pers. comm., dig. photo!]), are hybrids between that taxon and the Strigose Group (319 Lantana 1!), or are elements of *L. horrida*

Kunth (319 Lantana 1-C!, 1-D!, and 320 Lantana lα![the latter possibly hybridized with the Strigose Group]). Moreover, an unnumbered Herb. Cliff. sheet (!) is an element of the Strigose Group (*L. splendens* Medik.).

Linnaeus did not see the vouchers for the syntype illustrations. One of these (icon in Plukenet, Phytographia 385. t. 114, f. 4. 1691. [Voucher: 98:143 top-left specimen, BM-SL!]), belongs to the Setose Group (*L. hirsuta* M. Martens & Galeotti). The Commelin syntype has no known voucher (*C. Jarvis*, pers. comm.), illustrates only an inflorescence, and cannot be placed to trichome-morph. Even so, the trichome characters may not have been of much concern to Linnaeus. For example, in 1767, he did segregate *L. mista*, which has distinctly hispid twigs, as depicted in a Dillenius plate (see App. B), which he cited. However, Linnaeus did not use this character to differentiate the new species, but rather used the protracted leaf-blades, longer bracts, and capitula with mixed corolla colors. According to *C. Jarvis* (pers. comm.), no other original material is known.

To determine how this somewhat broad Linnaean concept was modified by later botanists, I present two lines of evidence. The first is a survey of sampled specimens to determine annotation patterns by taxonomists (Table 1, Fig. 5). The specimens are all those annotated by H. N. Moldenke as *L. camara* in LL/TEX (including the Moldenke Herb.) and BRIT/SMU, a selection of those at K, and a few for which I obtained photographs at BM, LINN, and OXF. Besides Moldenke, annotating authorities include: Linnaeus, Medikus (implied by citation, 1775), Schauer, Urban, Merrill, Hutchinson, R. Meikle, J. K. Morton, R. Fernandes, B. Verdcourt, G. Bromley, and S. Atkins. Dr. Méndez and I are excluded.

Plants annotated as *L. camara* (or in a few cases as L. aculeata, see App. B) were scored for whether trichomes on the abaxial surface were pilose-morph only, strigose-morph only, setose-morph only, or codominant mixtures of strigose- and pilose-morphs (including rare mixtures of strigose- and setose-morphs). Between the Linnaean period, when *L. camara* was applied primarily to pilose-morph plants, and the late nineteenth century, specialists began to apply the name primarily to the strigose-morph plants or those with mixed trichome morphs. For those annotated specimens from the neotropics, the mixed trichome plants are presumed hybrids primarily between the naturalized SCD cultigen and native species of the Pilose Group. In the paleotropics, the mixed-trichome plants appeared to be either 1) hybrids between escaped pilose-morph plants and the SCD cultigen, 2) escaped cultivars selected from hybrids between *L. camara* and various species of the Strigose Group, or 3) naturalized plants consisting of complex spontaneous hybrids between plants of the preceding two categories.

As this annotation trend developed, the plants of the Pilose Group began to be annotated with other later names. In particular, note the quotation of H. Moldenke [apparently in personal correspondence] by Howard (1969):

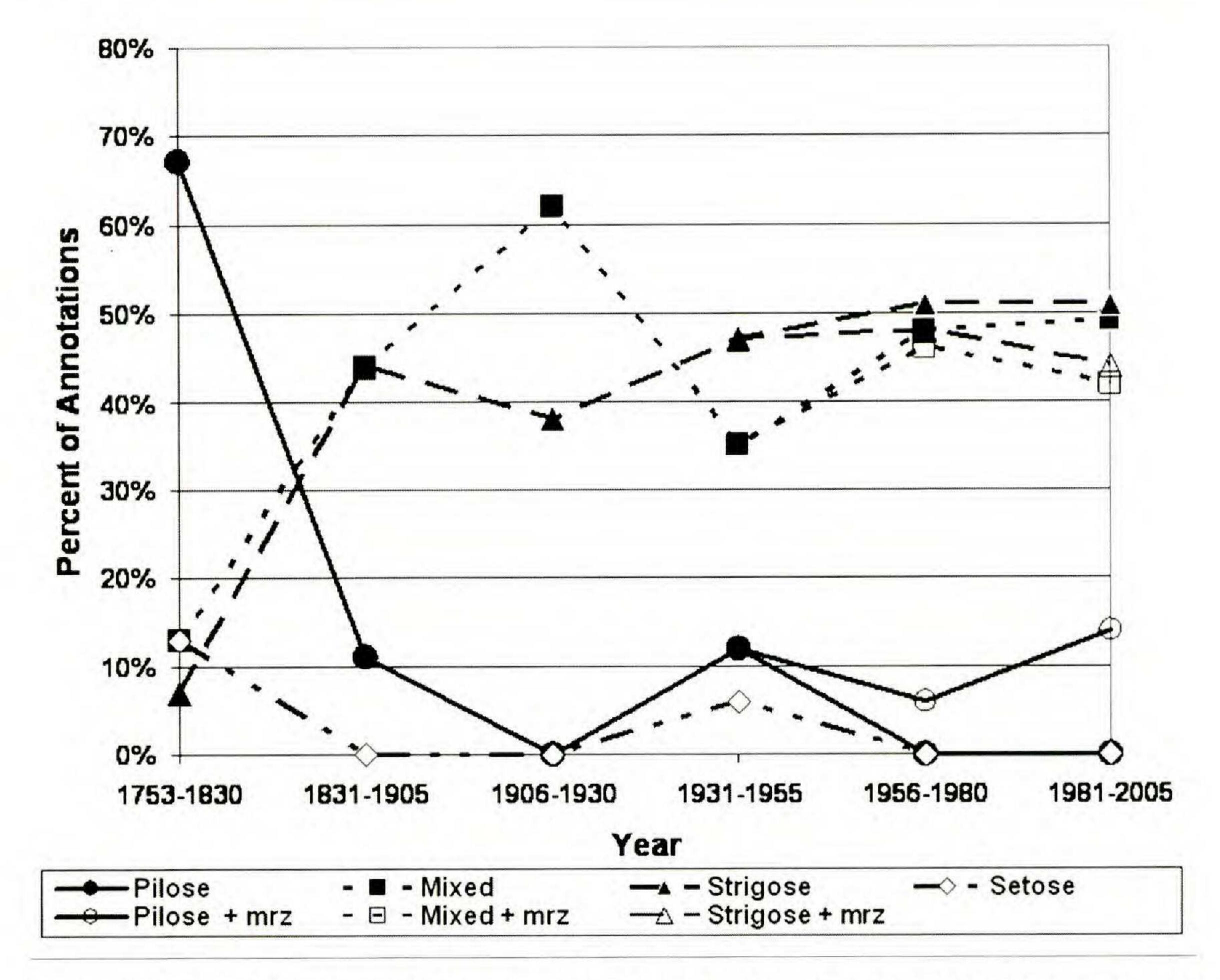


Fig. 5. Plot of portion of data from Table 1, showing historical pattern of specialists' application of the name Lantana camara to pilose-morph taxa (mostly L. camara, some L. horrida and their hybrids) vs. strigose-morph taxa (mostly L. strigocamara, L. nivea, and L. scabrida) vs. hybrids between the two groups (mixed morph plants) vs. setose-morph plants (mostly L. hirsuta). "+ mrz" indicates the inclusion of specimens annotated as L. camara var. moritziana.

You cannot depend on the accuracy of identification on the labels of plant specimens marked 'Lantana camara' in herbaria. I have found that a large percentage of such material is actually *L. moritziana*, *L. glandulosissima*, *L. scorta*, *L. horrida*, *L. arida*, *L. glutinosa*, etc. etc.

In other words, authorities (e.g., Moldenke and others) attributed specimens of *L. camara* to other species names referable to the Pilose Group. Surprisingly, in the mid 1970s, Dr. Moldenke accepted López-Palacios' (1974) reduction in rank of *L. moritziana* as a variety of *L. camara*. If that anomaly is excluded from the analysis, then the application of *L. camara* to strictly pilose-morph plants by taxonomic specialists is negligible over the last 50 years.

The second line of evidence is a survey of the literature (App. A). Adequate descriptions of leaf indument are scarce prior to the 1850s, but those by Medikus (1775), Sprengel (1825), and Schauer (1847, 1851) all indicate a prevailing acceptance of plants with the abaxial surfaces soft-hairy. The first publication diverging and treating strigose-morph plants as *L. camara* is by Otto and Dietrich (1841). This reflected a growing confusion as to what *L. camara* really is. By the

beginning of the twentieth century, most horticultural taxonomists took a broad concept of *L. camara* to include both pilose- and strigose-morph (or even setose-morph) plants in the species. This sentiment is reflected in Bailey's Cyclopedia (1900):

Lantanas have been long in cultivation, and it is difficult to refer the garden forms to botanical species. The species themselves are confusing. Most of the garden kinds are of the *L. Camara* type. There are several Camara-like species which probably have hybridized to produce these forms; but Voss [1896], the latest garden monographer, regards these species as only forms of *L. Camara* (preferring, however, to use the name *L. aculeata*). Accepting *L. Camara* in Voss's sense, the garden lantanas may be said to be derived from that species; and this view is adopted below.

Over the last 100 years, most floristic taxonomists (and hence, ecologists) have developed a similar attitude and broad concept or have followed Moldenke (1970) and Adams (1972), applying *L. camara* to the SCD cultigen and its hybrids, as has Sanders. Therefore, Mendez's other assertion that "Sanders (1989) attributed this binomial to a phenotype very different from prevailing opinion among the authors later to Linnaeus" is inaccurate.

Disparity between the lectotype and current use

The disparity between the lectotype and current use can be viewed in two ways. Either the current usage 1) includes the type and encompasses both pilose- and strigose-morph plants, or 2) excludes the type and is applied only to the SCD cultigen (and its hybrids with other species). The first view is problematic because the SCD cultigen behaves as a species distinct from the species named *L. camara* by Linnaeus. The second view raises the issue of relectotypifying *L. camara* to fit current usage. This might be preferable if LINN 783.4 were a horticultural hybrid no longer extant. However, the type is an element of a widespread wild species to which the name *L. camara* has been properly applied, at least in part, by taxonomists Standley (1924), Leon & Alain (1957), Macbride (1960), Gibson (1970), Nash & Nee (1984), López-Palacios (1977), Méndez (2002), and many ecologists. Futhermore, neither original material nor vouchers for cited illustrations consists of the SCD cultigen, and most of these specimens are of the pilose-morph (see preceding section). Therefore, overturning the choice of LINN 783.4 is not supported.

Correct name of the widespread SCD cultigen

To rectify the common practice of misapplying the name *Lantana camara* to the widespread SCD cultigen and to implement Méndez's recommendation that "...the system established by Sanders around *L. camara* should be reinterpreted," an attempt has been made to locate, to examine and, when needed, to choose nomenclatural types of all other published names in sect. *Lantana* (App. B). The results demonstrate that other names, also, have been misapplied by a number of specialists, including Schauer, Moldenke, Sanders, and Méndez.

With regard to the abaxial leaf indument, the SCD cultigen is essentially

outside the range of variation of *Lantana camara* but within the range of the Strigose Group (Fig. 4, 12). Thus, it would be imprudent to submerge this widely naturalized, aggressive species of hybrid origin as an infraspecific taxon of *L. camara*. Rather, the SCD cultigen more likely has a complex parentage involving *L. nivea* Vent., *L. scabrida* Sol. *in* Aiton, and *L. splendens* of the Strigose Group, as well as *L. camara*, and possibly other species (noteably, *L. hirsuta* of the Setose Group). Morphologically, it retains only the leaf shape and adaxial surface dullness of *L. camara*. Given the protracted history of collection and publication of new taxa, it is surprising that none of the available names can be verified as applying to this widespread cultigen. Apparently, this is due to there being so many published names and to the confused state of the taxonomy of sect. *Lantana*.

Through uncritical analysis of vague descriptions, one could argue that a few of the names that lack known types could be applied to the cultigen. However, taxonomic stability is more important than unsubstantiated priority. Assigning a neotype to a name whose concept can never be known with certainty in order to honor early taxonomists, who never understood the complexity of these plants, would be imprudent. Such names were never taken up and have no precedence of usage in the horticultural and ecological communities that taxonomists attempt to serve.

As a species of hybrid origin, of which that origin remains obscure, the SCD cultigen must be treated as a *species nova*. To provide taxonomic and bibliographic continuity, thus maximizing stability, the new epithet proposed here is based on the root "-camara." To indicate its hybrid nature and complex hypothesized parentage involving several species of the Strigose Group, it is given the prefix "strigo-"to produce *Lantana strigocamara*. At least two infraspecific epithets, and perhaps others, could serve as basionyms. However, epithet priority is mandatory only within rank, and I chose a new species name. *Lantana camara* L. var. *rubella* Moldenke (1949) is not widely known, and applying it to the whole of the species would broaden Moldenke's concept considerably. *Lantana flava* Medik. f. *sandersii* Méndez (2002) is only four years old and has not been taken up outside Méndez's own work. Raising it to species level would be tantamount to honoring myself.

Lantana strigocamara R. W. Sanders, sp. nov. (**Fig. 4**). Type: U.S.A. Florida: Dade Co.: near intersection of Montgomery St. and Old Cutler Rd, Montgomery Botanical Center, disturbed edge of rock pineland, 23 Sep 1981, *Sanders 1450* (HOLOTYPE.: FTG! [Dig. photo! see Fairchild Tropical Botanic Garden 1999]; ISOTYPE: NY!; Drawing, Sanders 1987, fig. 9).

Credita hybridogena de Lantana camara L. et L. nivea Vent. et L. scabrida Sol. in Aiton et L. splendenti Medik. et L. hirsuta M. Martens & Galeotti mixta simulat speciem. Differt a Lantana camara laminis foliorum subtus strigosis, trichomatibus remotis non nisi nervis mediis secondariis tertiariisque insidentibus angustate conicis antrorse geniculatis; a L. nivea et L. scabrida et L. splendenti laminis magis rugosis, base abruptius contractis, pinninervibus, superficiebus hebetibus haud nitidis; a L. nivea trichomatibus longioribus magis conspicuisque, corollis effectis pigmentis flavis vel aureis; a

L. hirsuta trichomatibus laminarum subtus nonsetiformibus angustate conicis antrorse geniculatis; a L. depressa Small (specie similari) laminis nec oblongis nec ellipticis haud conduplicate incurvatis amplisque, bracteis angustioribus attenuatisque, capitulis amplis.

Strict to lax, branched, erect, rounded or scandent shrub to 3 m tall (climbing much higher in some areas of the paleotropics); twigs hirtellous, angled, with or without prickles. Petioles 5–10 mm long; blades cordate to ovate, 3–10 \times 2–6 cm, mostly 1-1.7 times longer than wide, the base abruptly narrowed onto petiole, the apex acuminate, moderately rugose between higher orders of veins, dull above; hairs of adaxial laminar surface 0.3-0.7(-1.2) mm, scattered, in the form of antrorse strigae, often from pustulate bases; hairs of abaxial laminar surface usually 0.5 mm or less, stout, in the form of attenuately conical, geniculately antrorse strigae, but not closely appressed to surface, not deciduous, usually restricted to and scattered on midrib, secondary and tertiary veins (in some populations small erect hairs 0.1-0.2 mm long weakly developed on smallest veins and along crevice under larger veins); abaxial sessile glands green or not visible with 10× lens; teeth 15-25 per side, obtuse to short-acuminate, not revolute. Inflorescences 2-3 cm in diameter; peduncles 2-10 cm long; receptacle fistulose; bracts mostly 3-8 mm long, subulate, long-triangular or narrowly lanceolate (single outer series sometimes longer and narrowly spathulate or rarely subfoliaceous), apically attenuate, puberulent or hirtellous abaxially only, deciduous in fruit. Calyx 3 mm long, membranous; corolla yellow, orange-red, white, or pink to deep reddish purple and often mixed with orange or crimson, the throat often yellow, the tube 7-12 mm, slightly curved, the limb 6-10 mm across. Drupe ca. 5 mm across, blue-black; endocarp obovoid, inflated.

Paratypes: BURMA: Chantaburi, Makam forest, 26 Aug 1966, Larsen et al. 1841 (AAU, LL!). CHINA. Kwangsi: Kweilin, cult., 1979, Wan & Chow 79180 (LL!). INDIA. Lucknow, cult., 28 Oct 1974, Shivarajan 85750 (LL!). PAPUA NEW GUINEA. East Sepik Dist.: Wewak, 31 Aug 1968, Krauss 1287 (LL!). SRI LANKA. Sabaragamuwa Prov.: Kegalle: Kalugahatenne, 12 Feb 1974, Moldenke et al., 28331 (LL!,US!). UGANDA. Paraa, 29 Jul 1972, Moldenke & Moldenke 26073 (LL!). USA. Florida. Dade Co.: Homestead, 18 Jul 1966, Smith Fl. 6 (BRI, LL!). New York. Westchester Co.: Yonkers, cult., 23 Sep 1950, Moldenke 21133 (LL!).

Hypothesis of the history of the cultivated Lantana camara complex

Prior to the Linnaean period, the following species (citations in App. B) were already in cultivation in Europe, as deduced from the Sherard specimens at OXF, the Sloane and Clifford Herbaria at BM, and the Linnaean Herb. at LINN and S:

Pilose group Lantana camara (Fig. 1, West Indies and Mexico to northern South America)

Lantana. horrida (Fig. 8, including L. tiliifolia, Mexico to Argentina)

Strigose group Lantana nivea (Fig. 7, southern Brazil to Argentina)

Lantana scabrida (Fig. 2, West Indies, Mexico)

Lantana splendens (Fig. 6, Bahamas)

Setose group Lantana hirsuta (Fig. 3, Mexico)

All these species, except L. nivea, are characterized by capitula single in the leaf axils with stout peduncles and with corollas opening yellow and changing

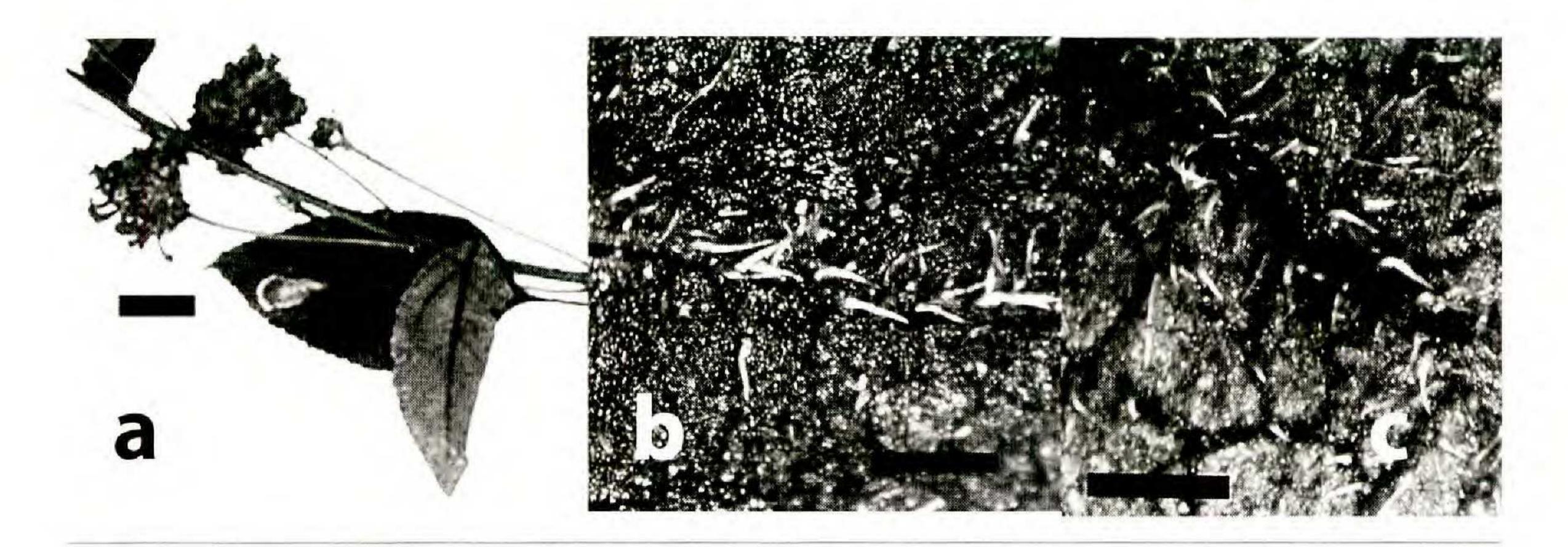


Fig. 6. Lantana splendens, epitype (Herb. Sherard 1269, OXF), **a.** inflorescence and representative leaves. **b.** adaxial leaf surface. **c.** abaxial leaf surface. Scale bars: a = 1 cm; b & c = 1 mm. Photographs supplied by OXF and used by permission.

to darker yellow, orange, or red-orange, and are aculeate or not. To my knowledge, Lantana nivea is exceptional among the natural species in having capitula commonly paired in the leaf axils with filiform peduncles and with corollas opening white and aging bluish, rose or purple, or opening pink and aging purplish. The plants are usually aculeate with recurved prickles, sometimes fiercely so. Therefore the only source in the cultivated complex for capitula opening yellow or cream and changing to purplish reds or orange plus purple would be hybridization between L. nivea and one or more of the other species. Parentage involving L. nivea is also consistent with stoutly recurved prickles in some of the cultivated hybrids. Apparently by backcrossing L. camara into such hybrids, plants with the mixed-colored capitula were developed within the range of variation of L. camara with respect to other characters (Fig. 9). Such plants I consider to be the subspecies combination L. camara subsp. aculeata. I am recognizing subspecies here and elsewhere in the complex for the following reasons: 1) the rank varietas in Lantana sect. Lantana has been overused for cultivars, and the varietal names are largely misapplied; 2) there may be yet undiscovered variety epithets that would take priority and further destabilize the nomenclature; and 3) I recognize the subspecies rank for geographically widespread infraspecies that comprise varieties, and further research will likely reveal localized geographic races that may warrant recognition at the rank of varietas. According to the ICBN (Greuter et al. 2000), this hybrid taxon cannot be treated as a nothosubspecies, but rather Art H3.3 would require treating it at the nothospecies level. However, it does not behave as a species distinct from L. camara, and it is the major representative of the species where it is naturalized, thus, simulating a widespread natural subspecies.

Lantana camara L. subsp. aculeata (L.) R.W. Sanders, comb. & stat. nov. (Fig. 9).

Basionym: Lantana aculeata L., Sp. Pl. 627. 1753. Lectotype designated by Méndez & Cafferty (2001, see App. B).

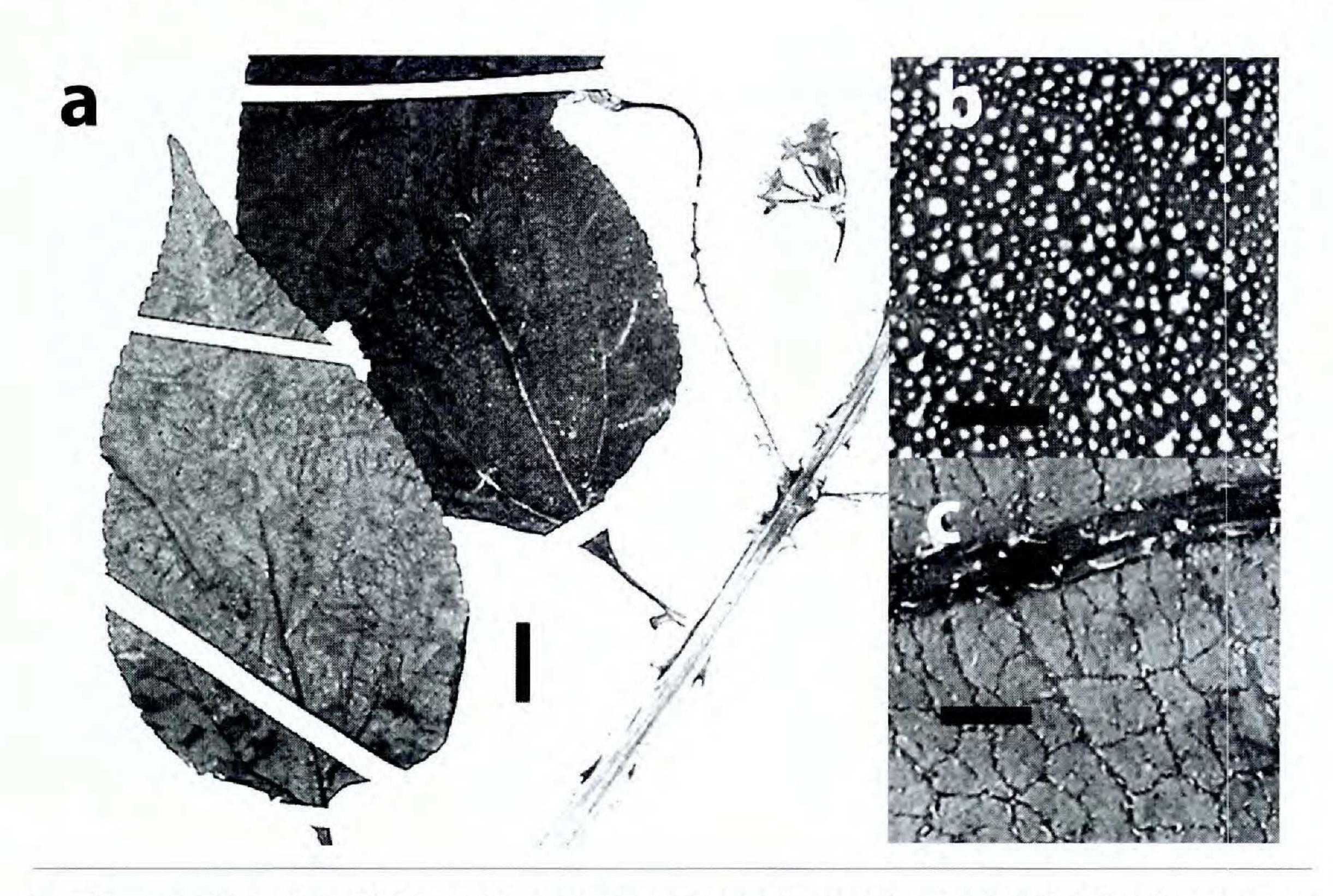


Fig. 7. Lantana nivea, epitype (Siebke s.n., C), **a.** stem, representative leaves, inflorescence with peduncle, and inset of inflorescence. **b.** adaxial leaf surface. **c.** abaxial leaf surface. Scale bars: a = 1 cm; b & c = 1 mm.

Likewise, backcrosses of *L. nivea* into the original mixed-color hybrids produced multicolored plants within the range or extending the range of variation of *L. nivea* with respect to other characters. Such plants I consider to be the subspecies combination *L. nivea* subsp. *mutabilis*. It is not treated as a nothotaxon by similar reasoning.

Lantana nivea Vent. subsp. mutabilis (W.J. Hook.) R.W. Sanders, comb. & stat. nov. Basionym: Lantana nivea Vent. var. mutabilis W.J. Hook., Bot. Mag. 5: pl. 3110. 1831. LECTOTYPE (here designated): icon in W.J. Hook., Bot. Mag. 5: pl. 3110. 1831.

Lantana nivea subsp. mutabilis may have been an important genetic vector for the origin of *L. strigocamara*. Even so, this taxon is not to be identified with *L. strigocamara* regardless of Bailey's (1900) and Moldenke's (1980b) having combined this taxon under *L. camara* and applying it to *L. strigocamara* (Moldenke in sched.) (see *L. amethystina* and *L. mutabilis* Lippold ex Otto & A. Dietr, App. B.).

The array of species names, dating from the Linnaean and early post-Linnaean period, that apply to hybrids (App. B, Fig. 12) shows the extent to which horticultural hybridization was complicating the systematics of this group. Lantana camara subsp. aculeata was hybridized at least with L. horrida (producing L. × mutabilis C. E. Weigel), with L. hirsuta (L. × mista L., Fig. 10), and with L. strigocamara or some undetermined species or species hybrids from the Strigose Group (L. × purpurea Hornem.). Lantana horrida was crossed with

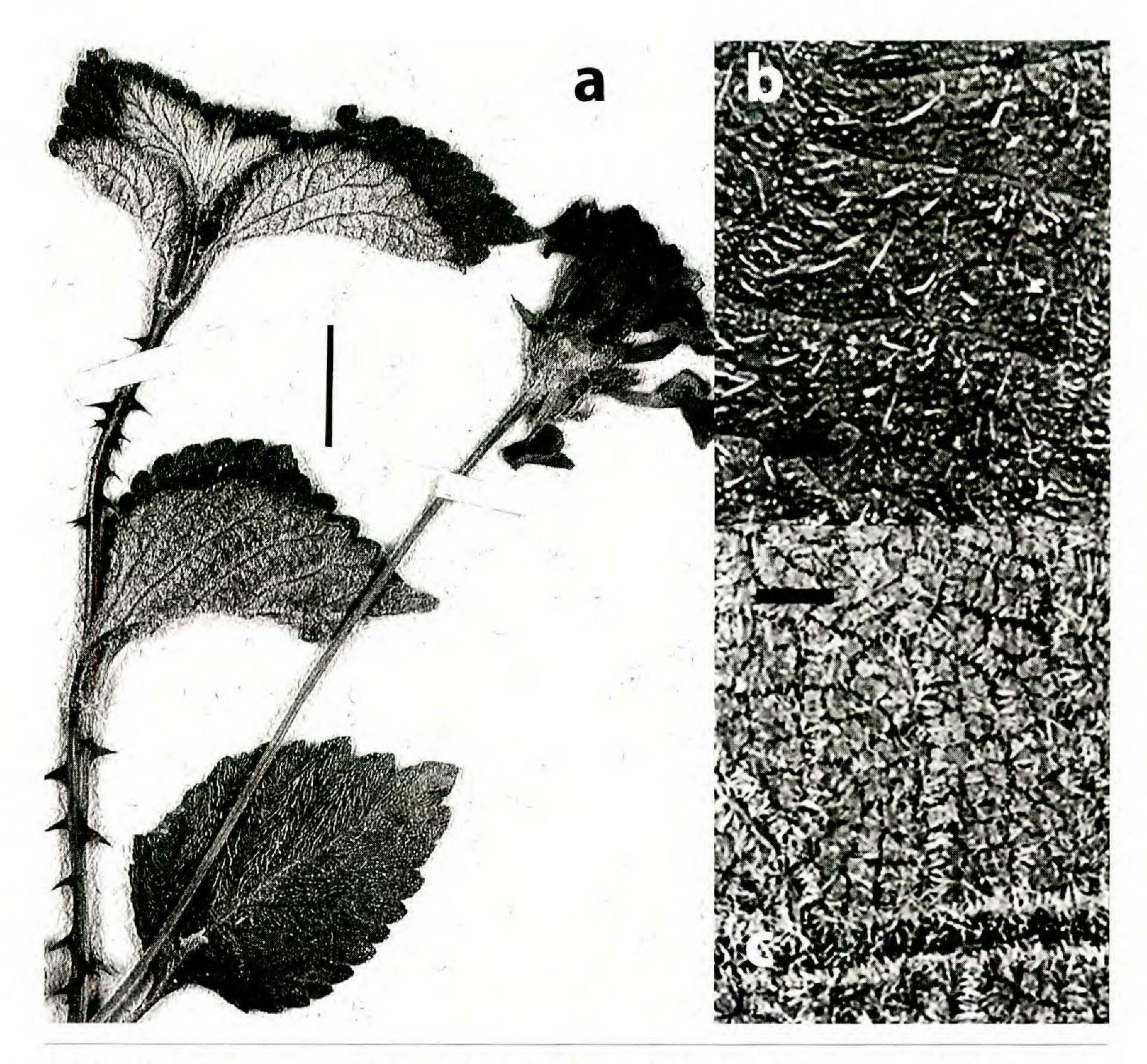


Fig. 8. Lantana horrida. **a.** portion of lectotype (Humboldt & Bonpland 4149, P-HBK, photograph provided by the Herbier National Paris [P], used with permission). **b**–**c.** representative specimen (Laughlin 1535, LL). **b.** adaxial leaf surface. **c.** abaxial leaf surface. Scale bars: a = 1 cm; b & c = 1 mm.

some of the species or hybrids of the Strigose Group to produce L. \times flava L. (Fig. 11). This latter hybrid appears to have mixed with backcrosses of L. nivea into L. camara subsp. aculeata (L. \times antidotalis Schumach. & Thonn.). Furthermore, within the Strigose Group, L. nivea was hybridized probably with L. scabrida or L. splendens to yield L. \times multiflora Otto & A. Dietr.

At about this time, these various hybrid plants were being introduced and naturalized throughout the tropics, especially as colonists settled in the West Indies, India, South Africa, Indonesia, Australia, and Pacific Islands. In some cases, the hybrids underwent polyploidy resulting in cultivated and escaped plants that grew aggressively and genetically swamped the characters of other cultivated and escaped plants with which they crossed. Thus, over the next two centuries, the diversity of the wild escaped plants was reduced to a few aggres-

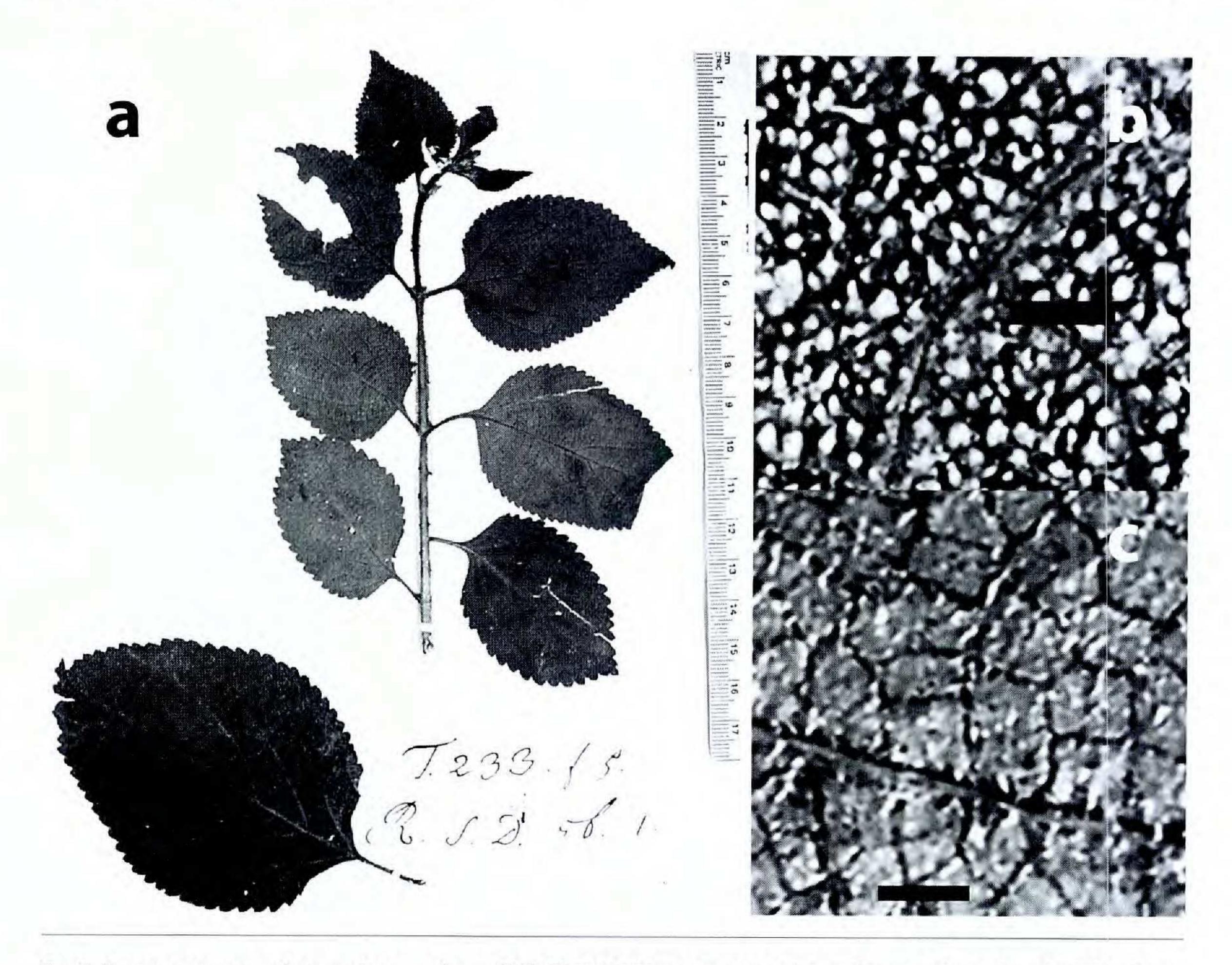


Fig. 9. Lantana camara subsp. aculeata, epitype (BM-SL 98: 143 bottom center). a. whole specimen. b. adaxial leaf surface. c. abaxial leaf surface. Scale bars = 1 mm.

sive cultigens and the recombinant variation expressed in hybrids between cultigens and in those between cultigens and indigenous species.

Apparently having originated along with the other early cultigens, *Lantana strigocamara* became one of the most widespread and aggressive. Clearly it was already escaped and crossing with native *L. urticoides* Hayek of Texas and *L. depressa* of Florida by the 1820s (see *L.×rubra* Berland. and *L.×floridana* Raf., App. B). *Lantana strigocamara* probably originated as a diploid, because diploid cultivars, usually given names such as 'Dwarf Yellow,' 'Dwarf Pink,' etc., are still available (Sanders 2001). However, post-origin allopolyploidy certainly has contributed to its aggressive growth and success in the wild. In introduced areas, it appears to have steadily increased in numbers, and by the early 1900s it came to dominate the occurrences among pantropical naturalized plants.

Howard (1969) pointed out that during the later half of the nineteenth century, lantanas lost popularity among horticulturalists. Most of the early hybrid cultivars apparently went extinct, except where escaped and naturalized in the absence of competition with *Lantana strigocamara*. However in the 1950s, lantana cultivars, developed primarily from a base of *L. strigocamara*, began to re-

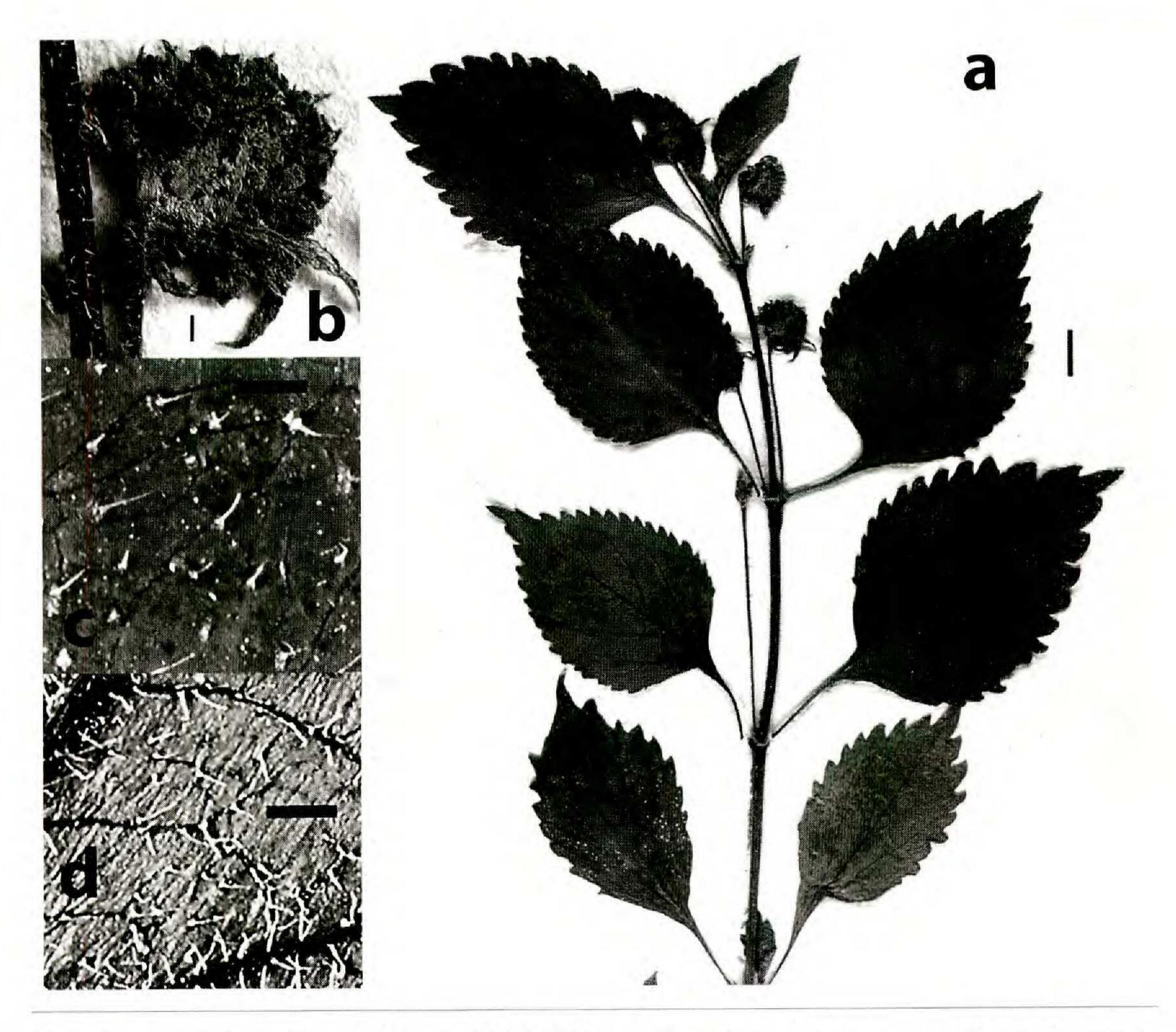


Fig. 10. Lantana \times mista, epitype (Herb. Sherard 1272, OXF). **a.** whole specimen excluding lowermost 4 cm of stem; note anomalous leaf-shape variation. **b.** inflorescence. **c.** adaxial leaf surface. d. abaxial leaf surface. Scale bars: a = 1 cm; b, c & d = 1 mm.

gain popularity, especially in seasonally dry subtropical areas where they can be used as drought tolerant borders. In particular, Monrovia Nursery in California crossed *L. strigocamara* with the very drought tolerant, persistently blooming *L. depressa* var. *depressa* of Florida to produce the now widely planted Callowiana Hybrids (Sanders 2001).

The Callowiana Hybrids apparently originated after autotetraploidy was induced in *Lantana depressa* var. *depressa*. The resulting tetraploid *L. depressa* would hybridize with tetraploid *L. strigocamara* to produce hybrids with an even balance of characters from both parents. This hybrid was then hybridized with various cultivars of *L. strigocamara* to generate an array of cultivars with a wide variety of floral color combinations, growth habits, and ploidal levels from triploid to hexaploid (Sanders 2001). The Callowiana Hybrids, thus, comprise a spectrum of variation completely connecting *L. strigocamara* and *L. depressa* var. *depressa*. This confusing variation led Moldenke (1975b) to name

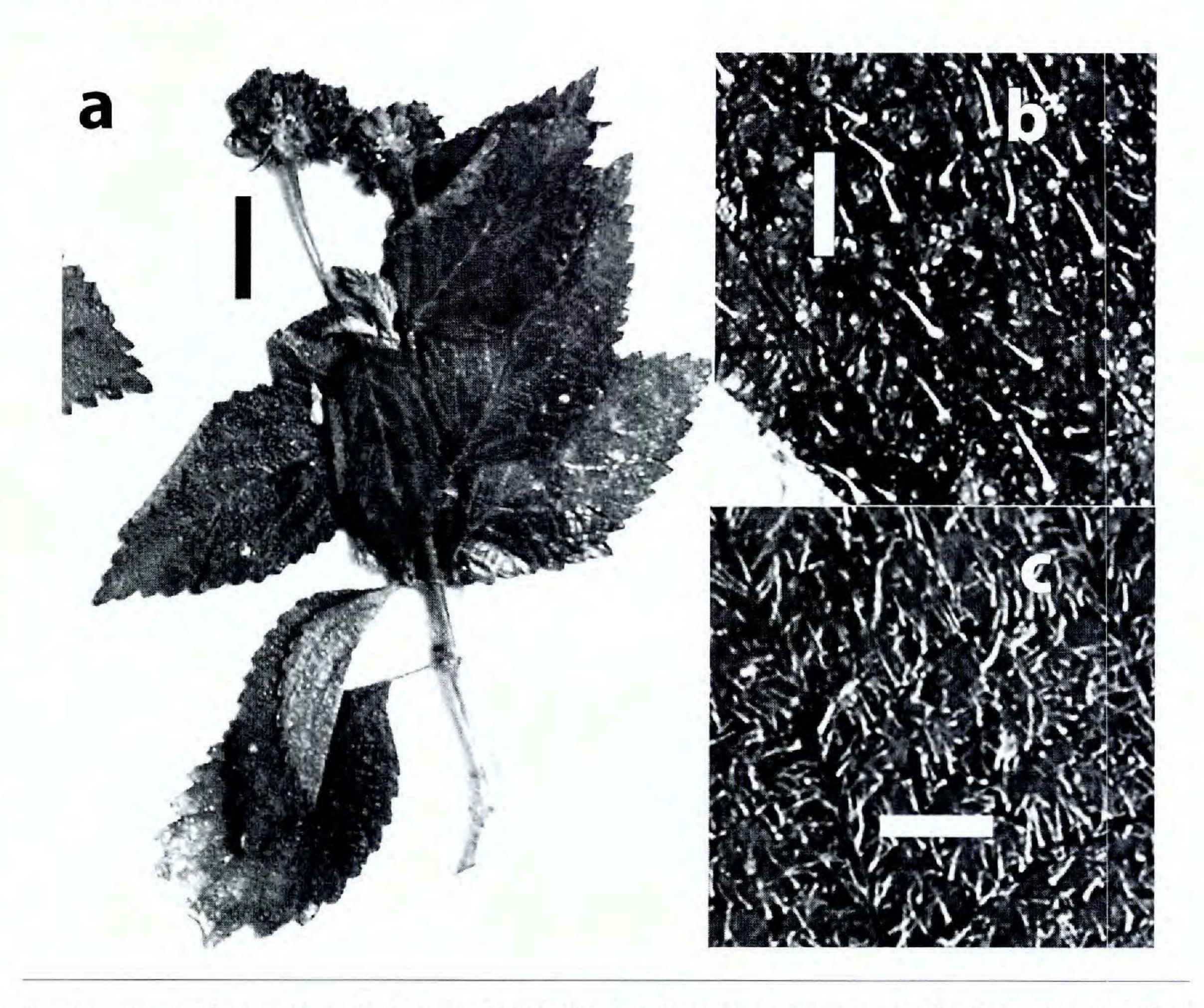


Fig. 11. Lantana \times flava, epitype (Herb. Sherard 1275, OXF). **a.** inflorescence and representative leaves. **b.** adaxial leaf surface. **c.** abaxial leaf surface. Scale bars: a = 1 cm; b & c = 1 mm.

one of these hybrids, probably Lantana cv. 'Cream Carpet,' as L. bahamensis f. albiflora.

CONCLUSION AND SUMMARY

The convoluted horticultural and natural history of *Lantana* sect. *Lantana* has resulted in highly complex systematic relationships of both cultivated plants and plants growing in the wild. Initial focus on cultivated forms during the Linnaean period resulted in an early proliferation of names for closely related cultivated plants and hybrids. These names clouded the taxonomy of naturally occurring species as plant exploration penetrated remote areas away from human population centers in colonial tropical America. Horticultural selection developed aggressively growing allopolyploid cultigen species and subspecies that became naturalized, often as pernicious weeds.

Even though *Lantana strigocamara* (i.e., the SCD cultigen), one of the most widespread and aggressive of these cultigens, is characterized predominantly by technical features of the Strigose Group, it became confused with *L. camara*

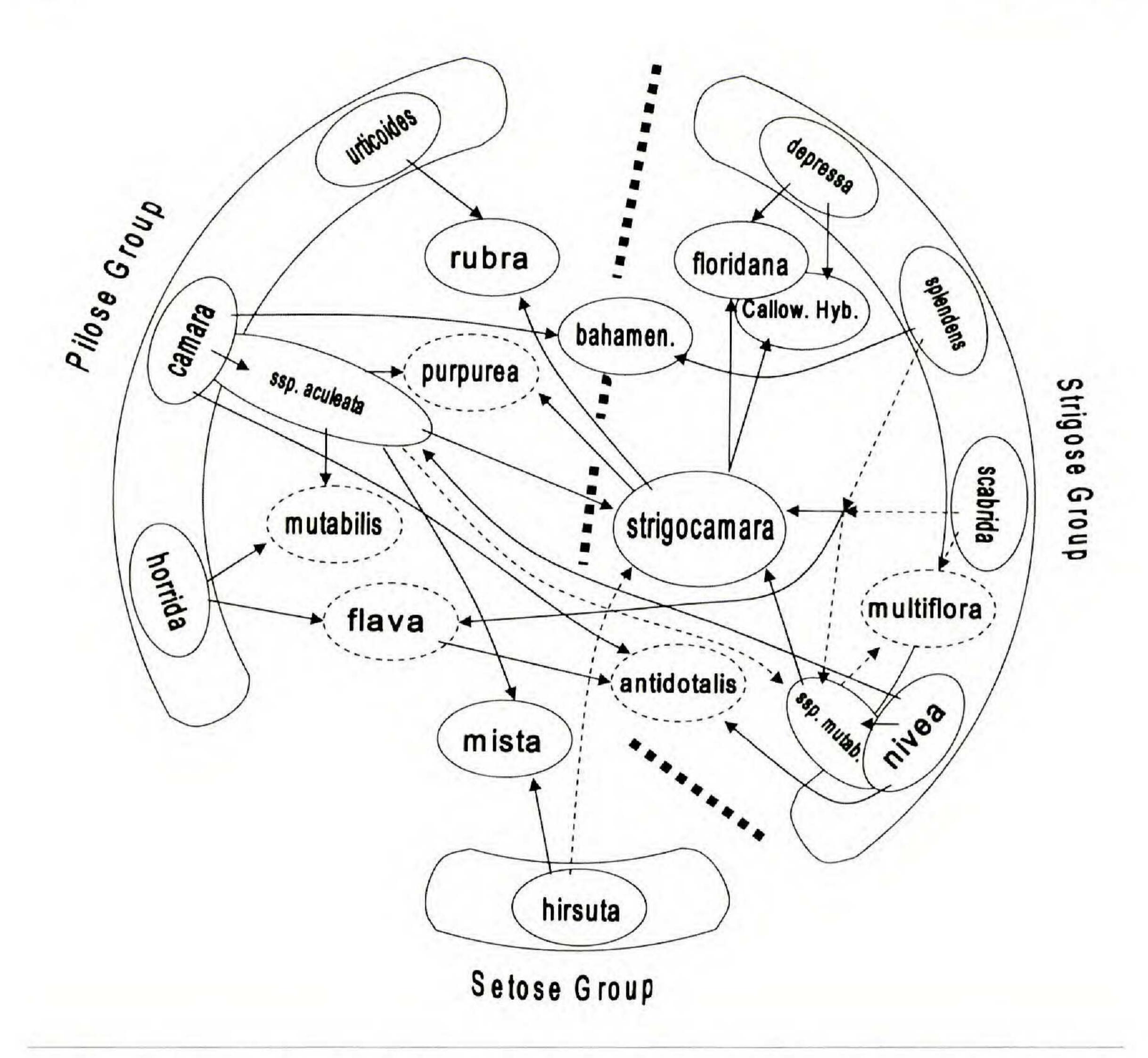


Fig. 12. Diagram showing relationships between natural species and named hybrids. Dashed ovals indicate hybrids that are extinct or rarely seen, either as cultivated plants or as naturalized escapes. Solid arrows indicate known or likely parentage based on admixture or intermediacy of morphological traits. Dashed arrows indicate alternate parentages deduced from characters that occur in several species or from sporadic development of diagnostic parental characters. The heavy dashed line separates the range of variation of the strigose-morph plants on the right from the pilose- and setose-morph plants on the left. The ' \times ' is omitted from hybrid names. For full names see Appendix B.

of the Pilose Group. Otto & Dietrich (1842) applied to one color variant of $Lantana\,strigocamara\,$ the name $L.\,mutabilis\,$ Lippold ex Otto & Dietr., but this is an illegitimate later homonym of $L.\,mutabilis\,$ C. E. Weigel, a name published for the distinct hybrid combination $L.\,camara\,$ subsp. $aculeata\times L.\,horrida\,$ (both of the Pilose Group). Sanders (1987a, b, c, 1989a, b, 2001) and Méndez (2002) both saw the need to treat the widespread SCD cultigen as a distinct species. Unfortunately, Sanders misapplied the name $L.\,camara\,$ to the SCD cultigen and the name $L.\,urticifolia\,$ to $L.\,camara\,$. Méndez correctly applied the name $L.\,camara\,$ but misapplied $L.\times flava\,$ to the cultigen. Thus, the SCD cultigen is newly named and described here as $L.\,strigocamara\,$.

As popularity of the original cultivars waned, later horticultural selection used a restricted set of aggressive polyploid hybrids, especially *Lantana strigo-camara*, as breeding stock; thus, this species of hybrid origin and its hybrids now strongly dominate the horticultural trade. Furthermore, where it has been introduced into tropical America, it competes or also hybridizes with indigenous taxa to produce a spectrum of variation challenging taxonomic research, which may be resolvable only with cytological and molecular techniques.

APPENDIX A

Use of name Lantana camara L. in taxonomic and horticultural literature in which trichomes are sufficiently described, in historical sequence.

Pilose-morph only

Medikus (1775) "folia...minus rugosa, mollioraque foliis Lantanae mistae" Sprengle (1825) "subtus albido-villosis"

Schauer, (1847) "subtus pallidis paginâ vel reti saltem brevi-villoso subcanescentibus"

Schauer, (1851) diagnosis = "subtus pallidis pagina v. reti saltem brevivilloso subcanescentibus" and description = "Foliorum indumentum variabile, magis pilosum et (subtus imprimis) magis tomentosum, magis minusve densum, tamen semper breve et in facie foliorum scaberrimum, e setulis antrorsis callo insidentibus confectum, neque hirsutum"

Troncoso (1965) "densamente villoso-pubescentes abajo" Note: Lantana camara does not naturally occur in Argentina. Thus, this description applies to escaped cultivars or to plants of Lantana horrida (incl. L. tiliifolia), L. micrantha, and L. riedeliana, which are native but submerged by Troncoso into L. camara.

Pilose- and strigose-morphs both included

Voss (1896) "oberseits scharf, unterseits blasser odor auf der Unterfläche oder ihrem Adernetz kurz-grauweiß-zottig." [inclusion of wide range of hair morphs clear from synonymy, included varieties, and use of "scharf" to modify "zottig."]

Bailey (1900) "pubescent beneath" [inclusion of wide range of hair morphs clear from synonymy and included varieties.]

Standley (1924) "variously pubescent or occasionally glabrate beneath"

Hutchinson & Dalziel (1931) "shortly pubescent below"

Bailey (1951) "pubescent beneath" [inclusion of wide range of hair morphs clear from synonymy and included varieties.]

LEON & ALAIN (1957) "el envés pubescente" [term equivocal, could be applied to both morphs] MACBRIDE (1960) "often canescently short-villous beneath" [presumes less pubescent morphs also included]

Gibson (1970) "variously pubescent beneath (densely viscid-tomentose to strigose or rarely glabrate)"

López-Palacios (1977) varying from "glabresentes" to "esparcido-pilosos o estrigulosos en el envés" to "corto-pubescentes por ambas caras"

Nash & Nee (1984) "el envés densamente viscido-tomentoso a estrigoso o hirsuto, raremente glabro"

Huxley (1992) "pubesc. above and beneath" [inclusion of wide range of hair morphs clear from synonymy and included varieties.]

Cullen et al. (2000) "downy or almost hairless underneath"

Strigose-morph only (or also mixed)

Otto & Dietrich (1841) diagnosis = "subtus hirtulis" and description = "oberhalb durch kleine Höckerchen scharf, etwas kurzhaarig, unterhalb *ebenfalls* [emphasis mine] zerstreut kurzhaarig, und etwas heller grün oder beinahe weißlich [glaucous?]" Note: They described *Lantana moritziana*, which is conspecific with true *L. camara*, as "Die Blätter...kurz-weichhaarig, nur wenig scharf und ziemlich weich anzufahlen." Furthermore, their description of *L. camara* is almost identical to theirs for *L. crenulata*, which Schauer (1847) described as "subtus pallidis, pubescenti-scabris."

Pearson (1912) "scabrid-pubescent above and on the veins beneath"

MOLDENKE (1970a) "short-pubescent, mostly on the venation beneath"

Long & Lakela (1971) "strigose beneath"

ADAMS (1972) "Lower surface of leaves thinly pubescent or almost glabrous" (as opposed to "with numerous short hairs")

MOLDENKE (1973b) "usually only sparsely pilosulous or strigillose beneath (mostly only on the venation) with canescent or brownish trichomes, sometimes glabrescent" [as opposed to "densely puberulent or short-pubescent"]

Correll & Correll (1982) "short pubescent, mostly on the venation beneath"

Moldenke & Moldenke (1983) "usually only sparsely pilosulous or strigillose beneath (mostly only on the venation) with canescent or brownish trichomes, sometimes glabrescent" Jansen-Jacobs (1988) "strongly or sparsely hirsute-strigose below, especially on the veins" Wagner et al. (1990) "lower surface sparsely short-pilose or strigillose, sometimes glabrate" Verdcourt (1992) "± pubescent or glabrescent beneath but scabrid on raised venation" Liogier (1994) "algo pelositas en el envés, a veces glabrescentes"

Pool (2001) "envés con tricomas estrigosos pequeños limitados a los nervios" [My work, as well as López-Palacios (1977) cited.]

APPENDIX B

Typification and history of application of names in *Lantana* sect. *Lantana*. Unless otherwise noted, herbaria given for authors and collectors in TL-2 (Stafleu & Cowan 1976–1988) were consulted for original material. An exhaustive search for isotypes was not attempted. Unless cited otherwise, handwriting comparisons based on Burdet (1979). A name is considered to be misapplied if the cited author or annotator clearly misunderstood the concept of that species and applied it to a species in such a way to exclude the type. A misapplication is inferred for publication of an infraspecific combination in which the infraspecific taxon actually belongs to a second species that excludes the type of the species under which the combination is made. The hybrid formulae for

nothospecies and species of hybrid origin are presumed parentages based on character combinations and intermediacy.

1753—Lantana camara L., Sp. Pl. 627.

LECTOTYPE (Moldenke & Moldenke 1983).—Cult, probably Hort. Uppsala, Herb. Linnaeus 783.4 (LINN!). (Fig. 1)

Name misapplied to:

- L. ×antidotalis (Verdcourt 1992)
- L. ×flava (Moldenke 1980b)
- L. horrida (Moldenke 1962, 1982c; Méndez 2002)
- L. × mista (Bailey 1900; Moldenke 1942)
- L. nivea (Bailey 1900; Moldenke 1955, 1980b)
- L. scabrida (Moldenke 1940, 1973b; Adams 1971)
- L. splendens (Moldenke 1976)
- L. strigocamara (Otto & Dietrich 1841; Moldenke 1940, 1949, 1970a, 1973b, in sched.; Long & Lakela 1971; Correll & Correll 1982; Sanders 1987a, b, c, 1989a, b, 2001, in sched.; Verdcourt 1992; Liogier 1994)

Taxonomic disposition.—L. camara (Pilose Group)

Discussion.—Linnaeus' concept of *L. camara* was developed from an array of garden and horticulturally selected plants. His reference in the protologue, in Sp. Pl. (ed. 2) 1763, and in Syst. Nat. (ed. 12) 1767 to synonyms that include the phrases "floribus miniatus," "flore variegata," and "flore variabile" indicates that garden hybridization had already introduced genes of at least *L. nivea* into the material he studied. However, the Moldenkes' lectotypification associated the name with an element characteristic of native Jamaican populations that lack the wider genetic variability and have only flowers opening yellow and changing to darker yellow, or at most, to reddish orange. Indeed, *Proctor 18266* (NY!) and *Yuncker 17043* (NY!), native material from Jamaica, are close matches to LINN 783.4.

Otto and Dietrich (1841) appear to have been the first to misapply *L. camara* to *L. strigocamara*. They described *L. camara* as having leaf blades (my translation) "basally somewhat rounded or almost cordate and having surfaces above with small, rough, sharp, somewhat short hairs, and likewise below scattered short-haired." They restricted the application to material of *L. strigocamara* with flowers opening yellow and aging orange (see also *L. crocea* [1804], *L. moritziana* [1841], *L. mutabilis* Lippold ex Otto & A. Dietr. [1842], and *L. variegata* [1842] below).

Sanders (1987c) explicitly excluded the type of *L. camara* by describing the species as having, "Hairs of abaxial laminar surfaces sparse, restricted mostly to midrib, secondary, and tertiary veins, stout, tapering-conical, geniculate toward base with distal 2/3 held parallel to lamina or vein surface."

1753—Lantana aculeata L., Sp. Pl. 627.

LECTOTYPE (Méndez & Cafferty 2001).— icon in Plukenet, Phytographia t. 233, f. 5. 1692.

Epitype (here designated).—Herb. Sloan 98:143 bottom center specimen (voucher of Plukenet, Phytographia t. 233, f. 5). BM-SL! (Fig. 9)

Name misapplied to:

L. camara (Medikus 1775; Méndez 2002)

L. camara × L. strigocamara (Méndez 2002)

L. horrida (Koch & Fintelmann 1858; Méndez 2002)

L. nivea (Méndez 2002)

L. strigocamara (Méndez 2002)

Taxonomic disposition.—L. camara (as L. camara subsp. aculeata)

Discussion.—To my knowledge, Schauer (1847) was the first author to place *L. aculeata* in synonymy under *L. camara*, which has equal priority, and his choice is followed.

Méndez and Cafferty chose Plukenet's figure as the lectotype. The voucher of the lectotype (i.e., epitype) is more or less within the range of variation of *L. camara* with regard to indument.

Although the abaxial surface hairs are sparser than is typical of Jamaican material, this condition is found in occasional native collections elsewhere. Linnaeus apparently developed the concept of *L. aculeata* to accommodate plants that were otherwise like *L. camara* but differed only by the development of prickles. As with *L. camara*, the protologue indicates both plants with yellow flowers changing only to dark yellow and those with flowers opening yellowish changing to red or purplish. In particular, Plukenet's phrase name includes "floribus miniatis." Not only the floral color variation (especially the late anthesis purplish pigments from *L. nivea*), but also the presence of prickles and sparse abaxial foliar hairs both point to hybridization influencing the wider variability in *L. aculeata*. Thus, my concept of the taxon is that of an infraspecific rank to account for all the cultivated and escaped plants of hybrid origin (regardless of floral color) falling within or slightly extending the range of variation of *L. camara*.

Méndez described *L. aculeata* as "abaxial surface with hairs relatively abundant, usually on all veins (including areoli), robust, conical, all, most, or at least a significant portion on the midrib, secondary or tertiary veins geniculate toward base and with distal 2/3 held parellel to vein surface, all those that grow on lower veins shorter and erect."To me, this describes hybrids between *L. camara* and *L. strigocamara*. Therefore, his application of *L. aculeata* to *L. camara* × *L. strigocamara* does not conform to the voucher of the lectotype, pointing out the need for epitypification. Furthermore, *L. aculeata* f. rubella (Moldenke) I.E. Méndez is to be identified with *L. strigocamara*, *L. aculeata* f. nivea (Vent.) I.E. Méndez with *L. nivea*, and *L. aculeata* f. parvifolia (Moldenke) I.E. Méndez with *L. camara*.

This taxon apparently was the main vector for infusing *L. camara* genes into the Strigose Group to produce *L. strigocamara*. It is not now widely available in the horticultural trade but appears to be rather widely naturalized in the paleotropics, especially Australia.

1767—Lantana mista L., Syst. Nat. ed. 12, 2:417.

LECTOTYPE (Méndez & Cafferty 2001).—icon in Dillenius, Hort. Eltham. t. 56, f. 64. 1732.

EPITYPE (here designated).—Herb. Sherard 1272. (voucher for Dillenius, Hort. Eltham. t. 56, f. 64) OXF! (Fig. 10)

Name misapplied to:

L. hirsuta (Schauer 1847, 1851 t. 42)

L. horrida (Méndez 2002)

Taxonomic disposition.—L. \times mista (L. hirsuta \times L. camara subsp. aculeata)

Discussion.—Reliance on the Dillenius figure led Méndez (2002) to associate this name with the wild species, *L. horrida*, which occurs in the Greater Antilles. However, when the epitype (i.e., voucher of the figure) is examined with reference to critical trichome characters, it is shown to be a hybrid between *L. hirsuta* and *L. camara* subsp. *aculeata*. It is not typical of *L. horrida*.

This hybrid combination is mostly of historical interest, as it is not now widely available in the horticultural trade and may have served as an agent for further hybridization and introduction of wider genetic variation into the cultivated complex.

1768—Lantana urticifolia Mill., Gard. Dict. ed. 8, Lantana 5.

Lectotype (Sanders 1989a).—Mexico. Edo. Veracruz: Veracruz, Houstoun s.n., Herb. Sloane 6:84. (BM-SL [dig. photo!, mounted photos NY!, UC!]).

Name misapplied to:

L. camara (Moldenke in sched.; Adams 1971; Sanders 1987b, c, 1989a, b; Liogier 1994)

L. horrida (Adams 1971; Sanders 1987b, 1989a)

Taxonomic disposition.—L. camara (see 1753)

Discussion.—Mark Spencer (Linnaean Typification Project, pers. comm.) verified that Herb. Sloane 6:84, collected by Houstoun at Veracruz, Mexico, is the only specimen bearing Miller's polynomial and is the only known original material of *L. urticifolia*. Nash & Nee (1984) cited the collection as "type" but questioned its existence at BM. Based on a mounted photograph at UC of the specimen at BM, Sanders (1989a) cited the specimen as "holotype" which is to be corrected to "lectotype."

Because Sanders (papers cited above) had misapplied *L. camara* so as to exclude its type, he applied the name *L. urticifolia* to provide a species name to all members of *L. camara*. In his concept of *L. urticifolia*, he also included the species *L. horrida*, here regarded as distinct.

1775—Lantana flava Medik., Hist. & Commentat. Acad. Elect. Sci. Theod.-Palat. 3. Phys. 225.

LECTOTYPE (here designated).—icon in Dillenius, Hort. Eltham. t. 57, f. 66. 1732.

Epitype (here designated).—Herb. Sherard 1275 (voucher for Dillenius, Hort. Eltham. t. 57, f. 66). OXF! (Fig. 11)

Name misapplied to:

L. camara (Schauer 1847; Koch & Fintelmann 1858)

L. scabrida (Méndez 2002)

L. strigocamara (Méndez 2002)

Taxonomic disposition.—L. \times flava (L. horrida \times L. spp. Strigose Group)

Discussion.—There is no indication on the Sherard specimen that Medikus saw it, and his description closely parallels Dillenius'. Because the protologue cites only Dillenius' name in synonymy, the Dillenius plate must be the type.

The protologue clearly describes the lower leaf surface as "pallidiora, tomentoso-pilosa." In bearing the mixture of long and short appressed hairs on the foliar upper surface and mixture of antrorse strigae with softer, filiform hairs on the lower surface, the epitype (i.e., voucher of the lectotype) agrees with the protologue and confirms that the parentage consists of *L. horrida* and one or more species of the Strigose Group. Therefore, it is not clear why Méndez (2002) chose to apply this name to material of *L. strigocamara*. He cited neither the plate nor its voucher.

This hybrid combination is mostly of historical interest, as it is not now widely available in the horticultural trade and may have served for further hybridization and introduction of wider genetic variation into the cultivated complex.

1775—Lantana splendens Medik., Hist. & Commentat. Acad. Elect. Sci. Theod.-Palat. 3. Phys. 226.

LECTOTYPE (here designated).—icon in Dillenius, Hort. Eltham. t. 57, f. 67. 1732.

Epitype (here designated).—Herb. Sherard 1269 (voucher for Dillenius, Hort. Eltham. t. 57, f. 67), left hand stem. OXF! (Fig. 6)

Name misapplied to:

L. strigocamara (Moldenke & Moldenke 1983)

Taxonomic disposition.—L. splendens (Strigose Group)

Discussion.—The lectotypification by Moldenke & Moldenke ([Dillenius s.n., OXF] 1983) is rejected as both imprecise and incorrect. The protologue cites as original material only the Dillenius name and plate as a definite synonym and a Plukenet name and plate as a questioned synonym. Not only does Medikus' description closely parallel Dillenius', but the voucher is not annotated by Medikus. Therefore, there is no evidence that Medikus studied the specimen, and the Dillenius plate is chosen as lectotype. Both the protologue and the epitype (i.e., the voucher of the lectotype) match native material from the Bahama Archipelago, the provenance given by Dillenius.

1775—Lantana sanguinea Medik., Hist. & Commentat. Acad. Elect. Sci. Theod.-Palat. 3. Phys. 229.

Type.—Unknown.

Name misapplied to:

L. camara or L. × mista (Schauer 1847)

Taxonomic disposition.—L. camara subsp. aculeata (see 1753) or L. X mista (see 1767)

Discussion.—Medikus cited no synonyms, illustrations, or specimens that could serve as type. His own herbarium is unknown. His description of trichomes is scant, making clear application of the name difficult. He did relate it most closely to *L. aculeata* L.; thus, the assumption made here is that it is a color variant of that taxon or *L. mista* L., for which he gave a similar description, except for ultimate color of the corollas.

1776—Lantana mutabilis C. E. Weigel, Physiogr. Sällsk. Hand. 1:46.

LECTOTYPE (here designated).—Cult., Greifsweld Bot. Gard. ("H.Gryph."), Pyl s.n., Aug. 1774 (JE [dig. photo!]).

Taxonomic disposition.—L. X mutabilis (L. camara subsp. aculeata X L. horrida)

Discussion.—The protologue indicates that the material growing in the Greifsweld Botanic Garden was the basis of the new species. The 1774 collection by Pyl is the only original material found at JE and was annotated by Weigel (J. Mueller, JE, pers. comm.). Interestingly, Weigel cited Camara melissae folio, flore variabili Dill. (Hort. Eltham. 65, t. 56, f. 65), in synonymy. The voucher of the illustration (Herb. Sherard 1274, OXF!) also is a hybrid between *L. camara* subsp. aculeata and *L. horrida*.

1789—Lantana scabrida Sol. in Aiton, Hort. Kew, ed. 1, 2:352.

Lectotype (here designated).—Cult. Royal Bot. Gard. Kew, "Hort. Kew 1777," (Solander s.n.?) (BM!). (Fig. 2) Taxonomic disposition.—L. scabrida (Strigose Group)

Discussion.—The specimen at BM apparently is the only original material. It is annotated "Hort Kew 1777" in an unknown hand, possibly Solander's, and "Lantana scabrida Ait. Hort. Kew ii 352!" possibly by J. Britton (M. Spencer, BM, pers. comm.). The only material cited in the protologue is "Nat. of the West Indies, Mr. Gilbert Alexander, Introd. 1774."

1789—Lantana melissifolia Sol. in Aiton, Hort. Kew, ed. 1, 2:352. nom. illeg. (superfluous)

LECTOTYPE (here designated).—icon in Dillenius, Hort. Eltham. t. 57, f. 66. 1732.

Epitype (here designated).—Herb. Sherard 1275 (Voucher for Dillenius, Hort. Eltham. t. 57, f. 66). OXF! *Taxonomic disposition.—L.* × *flava* (see 1775)

Discussion.—Solander cited Lantana flava Medik. in synonymy and cited the Dillenius plate. Evidence is lacking that he studied the voucher in the Sherard Herbarium.

1796—Lantana mutabilis Salisb., Prodr. Stirp. Chap. Allerton. 107. *nom. illeg.* (later homonym of *L. xmutabilis* C. E. Weigel)

Type.—None selected.

Taxonomic disposition.—L. camara subsp. aculeata (see 1753)

Discussion.—Because this is a later homonym of *L.* × *mutabilis* C. E. Weigel, it presents no problems. Based on the protologue, Salisbury appears to have named material with heads that change colors from yellow to purple. He cited only *L. camara* Linnaeus in Sp. Pl. (ed. 2) 1763 in synonymy; so, it is not clear whether he was assigning a substitute name or separating the material with multicolored heads as a new species.

1804—Lantana crocea Jacq., Pl. Hort. Schoenbr. 4:t. 473.

LECTOTYPE (here designated).—icon in Jacq., Hort. Schoenb. 4:t. 473.

Name misapplied to:

L. bahamensis (Schauer 1847; Koch & Fintelmann 1858)

L. camara (Otto & Dietrich 1842)

L. scabrida (Schauer 1847; Koch & Fintelmann 1858)

L. splendens (Schauer 1847)

Taxonomic disposition.—L. camara (see 1753)

Discussion.—No original material other than the plate has been found. The plate is a good match for many wild collected specimens from Jamaica. These differ from the type of *L. camara* only by details of leaf shape. However, herbarium samples suggests (unpubl. observ.) that, among Jamaican populations, leaf-shape variation is not correlated with geography or ecology.

Because Otto and Dietrich (1841, 1842) applied *L. camara* to *L. strigocamara* (see above), they applied *L. crocea* to *L. camara*, restricting its use to material with heads changing from yellow to orange and stems with prickles (see *L. moritziana*, 1841).

1804—Lantana nivea Vent., Jard. Malmaison t. 8.

LECTOTYPE (Here designated).—icon in Vent., Jard. Malmaison t. 8.

Epitype (here designated).—Cult., Paris "ex h. Paris, mis. Siebke," Siebke s.n, C! (Fig. 7)

Taxonomic disposition.—L. nivea (Strigose Group)

Discussion.—Ventenant provided a good description, excluding some details of leaf indument. Although the garden at Malmaison received material from gardens in the East Indies, it is clear that the description and plate apply to native material from southeastern Brazil, as noted by Schauer (1847). None of Ventenant's original material cultivated in Paris was located in B-WILLD, C, G, or P (no response from WU). A specimen found in C and cultivated in Paris was annotated as *L. nivea*, but apparently not in Ventenant's hand, indicating it not to be original material. Because subsequent authors have misunderstood this species as evidenced by the several new names described for more recent wild collections of this species, the specimen in C is designated as to support the icon. It clearly matches the protologue and was at Paris about the time of Ventenant such that the annotator should have been familiar with Ventenant's concept.

1815—Lantana purpurea Hornem., Hort. Bot. Hafn. 2:583.

LECTOTYPE (here designated).—Cult. Hort. Reg. Bot. Hafn. "1814" (C!). Name misapplied to:

L. camara (Schauer 1847; Koch & Fintelmann 1858; Bailey 1900)

Taxonomic disposition.—L. Xpurpurea (L. camara subsp. aculeata × L. spp. Strigose Group)

Discussion.—The lectotype is in a type folder marked as "specimina originalia" (also labeled as "IDC microfiche 111^{III 1-2}). The verso is annotated "Lantana purpurea Horne. 1814," presumably in Hornemann's hand, and stamped "Hb. Schum.." A second specimen (IDC microfiche 111^{II 7}) is annotated "Lantana purpurea h.h." in a different hand and stamped "Hb. Liebm." Both specimens are characterized by a mixture of erect and geniculate trichomes on the abaxial surfaces. The purplish corollas suggest that a purple-flowered cultivar of *L. camara* subsp. *aculeata* was crossed with a cultivar from The Strigose Group.

1817—Lantana hispida Kunth in HBK., Nov. Gen. Sp. 2:260.

LECTOTYPE (Nash & Nee 1984).—Mexico. Edo. Veracruz: "juxta Xalapam," Humboldt & Bonpland s.n. (P-HBK [dig. photo!, Macbride Neg. 39493 F!, BRIT!]).

Name misapplied to:

- L. hirsuta (Moldenke 1947, 1973b)
- L. hirta Grah., sp. sect. Callioreas (Schauer 1848; Koch & Fintelmann 1858; Standley 1924; Moldenke 1963, Gibson 1970)
- L. velutina Mart. & Gal., sp. sect. Callioreas (Moldenke 1982c)

Taxonomic disposition.—L. horrida (see next)

Discussion.—Schauer's misapplication of the name to *L. hirta* Graham in section *Calleoreas* has resulted in persistent confusion. Furthermore, the epithet is easily confused with *L. hirsuta* M. Martens & Galeotti, a distinct species. Therefore, in combining *L. hispida* with *L. horrida* as conspecific, I choose the latter in accord with ICBN Article 11.5 (Greuter et al. 2000).

1817—Lantana horrida Kunth in HBK., Nov. Gen. Sp. 2:261.

LECTOTYPE (Nash & Nee 1984).—Mexico. Distrito Federal: "monte Chapultepeque juxta urbem Mexici,." Humboldt & Bonpland 4149 (P-HBK [dig. photo!]). (Fig. 8a)

Name misapplied to:

L. × rubra (Schauer 1847)

L. urticoides (Moldenke 1942, 1961, 1970a, 1978)

L. hirsuta × L. camara (Moldenke 1982d)

Taxonomic disposition.—L. horrida (Pilose Group)

Discussion.—Berlandier 2310, annotated by Berlandier as Lantana rubra (L. urticoides \times L. strigocamara), a syntype of L. horrida var. parviflora Schauer, and the epitype of L. \times rubra (see below) was mistakenly included in L. horrida by Schauer (1847). As a result, Moldenke misapplied the name L. horrida to L. urticoides until correcting himself (Moldenke 1978).

1827—Lantana antidotalis Schumach. & Thonn. in Schumach., Beskr. Guin. Pl. 276.

LECTOTYPE (Junghans 1962.p. 94, as to collection; here designated as to duplicates).—Ghana, *Thonning* 125 (C [IDC microfiche ident. no. 64 13-4]!; ISOLECTOTYPE: C[IDC. no. 64 15-6]!).

Taxonomic disposition.—L. \times antidotalis (L. nivea \times L. camara \times L. \times flava?)

Discussion.—The duplicate most in accord with the protologue (leaf blades 2-3 inches long) is chosen as the lectotype. Though given the same collection number, these two specimens may actually represent two different populations as judged from slight morphological differences. Assigning hybrid status to this naturalized plant is based on the variable leaf shape and size (narrowly ovate-oblong or narrowly triangular; length 1.7 to 2.7 × width), subsetiform trichomes on the upper and lower leaf surfaces, and the mixture of erect and geniculate hairs on the lower leaf surfaces. The parentage probably includes *L. nivea* or *L. splendens* from the Strigose Group and *L. camara* and *L. × flava* from the Pilose Group.

1829—Lantana albopurpurea Desf., Tabl. École Bot., ed 3.393.

Lectotype (here designated).—Cult. Hort. Paris., "H. p." labeled "Herbarium Webbiana ex Herb. Desfontaines" (FI [dig. photo!]).

Taxonomic disposition.—L. X mista (see 1767)

Discussion.—The specimen at FI is clearly original material, as the annotation is in Desfontaines' hand (C.Nepi, pers. comm.). None other is known to me. The leaf indument suggests this specimen has the same parentage as does $L. \times mista$.

1829—Lantana suaveolens Desf., Tabl. École Bot., ed 3. 393. nom. illeg. (non L. suaveolens Spreng. = L. angustifolia Mill.)

Type.—Not investigated.

Taxonomic disposition.—probably L. camara or its hybrid (see 1753)

Discussion.—The description of prickly stems, ovate leaves, lanuginose bracts, and yellow flowers suggests this is an element of *L. camara*.

1832—Lantana rubra Berland. in Terán & Berland., Mem. Comis. Limites 15.

LECTOTYPE (here designated).—icon in Berlandier in Ohlendorf et al., transl. Journey Mex., t. 5 (top, facing p. 410). 1980.

Epitype (here designated).—*Berlandier 2310=880*, Mexico. Tamaulipas: Matamoros, GH! (isoepitype: NY!, none found at G under *L. rubra*).

Taxonomic disposition.—L. \times rubra (L. urticoides \times L. strigocamara)

Discussion.—The only original material known to me includes the recently published plate, which Berlandier either executed or supervised, and three sheets (Berlandier 2114=697 [GH!], 2310=880 [GH!, NY!]), which consist of hybrids. Although the protologue suggests L. urticoides (see 1906 below), the only native species in the region of the eastern Texas-Mexico boundary, all the original material lacks the rotund, large-toothed leaf blades and persistant fruiting bracts, characteristic of L. urticoides. Instead, they are intermediate between L. urticoides and L. strigocamara, which obviously had become well enough established by the late 1820s to produce spontaneous hybrids with L. urticoides. If any of the hybrid specimens were chosen as lectotype and other original material that actually belongs to L. urticoides should be found, such a lectotypification could be easily overturned. However, stability of the application of L. rubra and retention of L. urticoides as the correct name of the wild species is best served by accepting the plate as lectotype.

Of the two Berlandier gatherings know to me, 2114=697 is more typical of the hybrids, especially in the hoary young stems with spreading subsetiform hairs to 1.5 mm long. Berlandier 2310=880 has larger teeth and subpersistent bracts more like the L. urticoides parent, but the indument shows it to be a hybrid. It is chosen as epitype because it is annotated "Lantana rubra B," apparently in Berlandier's hand, is a syntype of L. urticoides var. parvifolia Schauer, and is represented by duplicates in major herbaria.

This hybrid combination is the typical cultivated plant in Texas and the Gulf Coast Plain of the Southeastern United States. It may have been propagated for the trade due to the cold hardiness arising from the Texas parent, *L. urticoides*.

Index Kewensis (Jackson 1895) cites "Lantana rubra Perr.," but this is a mistake as Perrottet (1825) actually referred to Latania rubra Jacq. (Arecaceae), the next entry in his list after Lantana.

1832—Lantana tiliifolia Cham., Linnaea 7:122.

LECTOTYPE (Santos Silva 2001).—Brazil: Bahia. *Sieber s.n.* (B-WILLD 11502 [dig. photo! Berlin Dahlem. 2005]).

Name misapplied to:

L. strigocamara or its hybrids (Moldenke in sched)

Taxonomic disposition.—L. horrida (see 1817)

Discussion.—The protologue lists three syntypes—the Sieber collection from Bahia, Brazil, Sellow collections ("southern Brazil...copious numbers from many locations and times," BR [dig. photo!]; NY!, fragment NY!), and Lhotsky s.n (n.v.). I disagree with the lectotypification by Santos Silva (2001). In the digital photograph of B-WILLD 11502 provided by B, the specimen appears to have mostly glandular hairs on the stems and petioles. The Sellow specimen at BR bears mostly non-glandular hairs. Chamisso's diagnosis mentions only "ramis...hirtis," although his description (my translation) indicates that the "upper stems have glandular hairs often but not always mixed in." Later, Poeppig segregated the strongly glandular plants as L. glutinosa (see 1842 below). Modern usage follows Poeppig in restricting L. tiliifolia to the non- or weakly glandular specimens. However, because I treat both L. tiliifolia and L. glutinosa as synonyms of L. horrida, further research is needed to determine whether a proposal to conserve a different type is needed.

1832—Lantana floridana Raf., Atl. J. 148.

Type.—Not found in DWC, FI, G, NY, P, P-DU, PH, PI, WIS, or WS; no response from LE, NAP, or W. Taxonomic disposition.—L. \times floridana (L. depressa \times L. strigocamara)

Discussion.—The only native wild taxon of the upper Atlantic coast of Florida is *L. depressa* var. floridana (Moldenke) R.W. Sanders (see 1905, below). However, the protologue describes the flowers as "versicolor, yellow, orange, red, crimson on same shrub." As discussed in Sanders (1987a), none of the varieties of *L. depressa* is characterized by the orange or red floral pigments. However, this does characterize hybrids between *L. depressa* and *L. strigocamara*, (the latter in Sanders 1987a as *L.* camara). In light of the hybridization between introduced *L. strigocamara* and native *L. urticoides* in Texas in the 1820s (see *L. rubra* 1832 above), *L. strigocamara* was likely also naturalized in Florida by that time, and Rafinesque's description refers to hybrids.

1838—Lantana antillana Raf., Sylva Tellur. 82.

Type.—Not found in DWC, FI, G, NY, P, P-DU, PH, PI, WIS, or WS; no response from LE, NAP, or W. *Taxonomic disposition.—L. horrida* (see 1817) or *L. camara* (see 1753)

Discussion.—Rafinesque noted this to be Lantana camara of authors and an Antillean shrub, which he saw living. He also noted that it differs from *L. floridana* primarily by the stem and leaves hirsute and the bracts ovate-lanceolate and concave. Neither of these characters appears to be consistent with this being an element of *L. strigocamara*.

1838—Lantana rosea Raf., Sylva Tellur. 83.

it in sect. Callioreas.

Type.—Not found in DWC, FI, G, NY, P, P-DU, PH, PI, WIS, or WS; no response from LE, NAP, or W. *Taxonomic disposition.*—probably *L. reticulata* Pers. or *L. involucrata* L. (. Sect. *Callioreas*) *Discussion.*—Even though Rafinesque placed this species in his subgenus Camara Raf., his subgenera are neither well demarcated nor consistent. He included *L. camara* L. in subgenus *Camara* Raf. and the conspecific *L. aculeata* L. in subgenus *Periana* Raf. (along with *L. involucrata*). *Lantana rosea* is described as a native Antillean plant with small roundish (but apically and basally acute) leaves, rounded cinerous stems, and short, ovate bracts, and rose-pink corollas, all of which appear to place

1838—Lantana incarnata Raf., Sylva Tellur. 83.

Type.—Not found in DWC, FI, G, NY, P, P-DU, PH, PI, WIS, or WS; no response from LE, NAP, or W. *Taxonomic disposition.*—probably *L. nivea* subsp. *mutabilis* (W.J. Hook.) R.W. Sanders (see 1804 and text, *L. amethystina* 1841)

Discussion.—By 'incarnate,' Rafinesque presumably meant that the heads are flesh-colored in bud, the corollas open cream and turn light or fleshy pink. This is consistent with some populations of *L. strigocamara*. However, the ovate-oblong leaf blades acuminate at both apex and base rule out *L. strigocamara*. The floral color, leaf shape, and long, linear-lanceolate bracts are all consistent with *L. nivea* subsp. *mutabilis*.

1839—Lantana coccinea G. Don, Hort. Brit., ed. 3. 245. nom. nud.

Type.—Unknown.

Taxonomic disposition.—L. camara subsp. aculeata?

1841—Lantana crenulata Otto & A. Dietr., Allg. Gartenzeitung 9:363.

Type.—Unknown (no original material known; if herbarium specimen from material cultivated in. Hort. Berlin [Otto s.n.,?] existed in B, now destroyed; Shauer [1847] indicated seeing a live specimen in Hort. Berlin).

Name misapplied to:

L. splendens (Schauer 1847)

Taxonomic disposition.—L. × antidotalis (see 1827) or L. scabrida (see 1789)

Discussion.—The protologue cites no original material, but the description strongly suggests L. scabrida or related species or hybrids in the Strigose Group. Identity with L. strigocamara is excluded because the leaves are described as pointed on both ends.

1841—Lantana moritziana Otto & A. Dietr., Allg. Gartenzeitung 9:369.

LECTOTYPE (Schauer 1857, as to gathering; here designated, as to specimen).—Venezuela. Caracas, *Moritz 163* (G [dig. photo!]; ISOLECTOTYPE: G [lacking inflor.,dig. photo!]).

Name misapplied to:

L. camara (Otto & Dietrich, 1841, 1842)

Taxonomic disposition.—L. camara (see 1753)

Discussion.—The protologue indicates nativity only by "Habitat in Caracas" without specifically citing the Moritz specimen. In his treatment, Schauer (1847) cited only Moritz 163 from Caracas, Venezuela, but stated that he saw cultivated and wild-collected herbarium specimens at B. The only duplicates of Moritz 163 known to me are at G. The one chosen as lectotype bears two annotation labels besides the collection label, all apparently in Schauer's hand. The duplicate at G lacks infloresences, is not annotated by Schauer, but is annotated by Moldenke as "Isotype." Macbride photographed material at B (neg. no. 17478, destroyed [photo F!, BRIT!, GH!]), which he may have thought was type material. The specimen is not signed by either Otto & Dietrich or Schauer, and it bears the date "1844." Therefore it cannot be considered a type, even though López-Palacios (1977) cited it as such.

Because Otto and Dietrich (1841, 1842) misapplied *L. camara* to *L. strigocamara*, they applied *L. moritziana* to plants of *L. camara* with no prickles and flower heads changing from yellow to orange.

1841—Lantana multiflora Otto & A. Dietr., Allg. Gartenzeitung 9:370.

Lectotype (here designated).—Cult.Hort.Berlin,Ottos.n.(B, destroyed [Macbride Neg. 17379 F!, BRIT!]). Taxonomic disposition.—L. \times multiflora (probably L. nivea \times L. scabrida or L. splendens)

Discussion.—Otto and Dietrich cited no specimen, but the destroyed specimen photographed by Macbride appears to have been the only original material. In general, the protologue suggests *L. nivea*; although, the more distinct scabrosity of the leaves suggest *L. scabrida* or *L. splendens*. The floral color, described further in Otto and Dietrich (1842) as lilac (in bud?) changing to yellow, clearly implicates genes of both *L. nivea* and yellow-flowered species of the Strigose Group.

1841—Lantana amethystina Otto & A. Dietr., Allg. Gartenzeitung 9:370.

Type.—Unknown (no original material known; if herbarium specimen from material cultivated in. Hort. Berlin [Otto s.n.,?] existed in B, now destroyed).

Taxonomic disposition.—L. nivea (as L. nivea subsp. mutabilis, see 1804 and text)

Discussion.—Otto and Dietrich (1842) indicated that this is a replacement name for *L. nivea* var. *mutabilis* W.J. Hooker. Apparently, Otto and Dietrich were not aware of *L. mutabilis* C.E. Weigel and *L. mutabilis* Salisb. but did consider that Lippold had named *L. mutabilis* Lippold ex Otto & A. Dietr. for a distinct species such that the Hooker varietal epithet was unavailable at the rank of species (see next entry).

1842—Lantana mutabilis Lippold ex Otto & A. Dietr., Allg. Gartenzeitung 10:314. *nom. illeg.* (later homonym of *Lantana* × *mutabilis* C. E. Weigel)

Type.—Unknown (no original material known; if herbarium specimen from material cultivated in. Hort.Berlin [Otto s.n.,?] existed in B, now destroyed; no material of Lippold found at RB [R. Campostrini F., pers. comm.]).

Taxonomic disposition.—L. strigocamara (see 2006 and text) or L. strigocamara \times L. camara subsp. aculeata

Discussion.—As noted under L. camara, Otto and Dietrich (1841) appear to have applied the name L. camara to the phenotypes of L. strigocamara having floral heads changing from yellow to orange. However, material of L. strigocamara with purplish and yellowish pigments occurring together they apparently described under L. mutabilis Lippold ex Otto & A. Dietr. As a later homonym, this name is not available for L. strigocamara.

1842—Lantana variegata Otto & A. Dietr., Allg. Gartenzeitung 10:314.

Type.—Unknown (no original material known; if herbarium specimen from material cultivated in. Hort. Berlin [Otto s.n.,?] existed in B, now destroyed).

Taxonomic disposition.—L. camara subsp. aculeata or L. camara subsp. aculeata \times L. spp. Strigose Group

Discussion.—No holotype or syntypes are cited; however, the protologue suggests cultivated material in the range of *L. camara* subsp. *aculeata* (see 1753).

1842—Lantana glutinosa Poepp. in Otto & A. Dietr., Allg. Gartenzeitung 10:315.

LECTOTYPE (López-Palacios 1977, as to gathering; here designated as to specimen).—Peru, *Poeppig 1375* (G-DC [dig. photo!]; duplicate, B?, destroyed [Macbride Neg. 34340 F!, BRIT!]; ISOLECTOTYPE: GH!). *Taxonomic disposition.—L. horrida* (see 1817)

Discussion.—Other than "Habitat in Peruvia," no material is cited and lectotypification is required. The Macbride photograph (Neg. 34340) is presumed to be of a specimen at B, since destroyed, although no herbarium identification is visible in the image. If this be true, it would have been the preferred lectotype.

1842—Lantana asperata Hort. ex Vis., Orto Bot. Padova 142. nom. nud.

Type.—Unknown.

Taxonomic disposition.—L. nivea? (see 1804)

Discussion.—Visiani merely listed the species as having been grown under this name at Hort. Parisiense, without intending to publish it as his own. He also stated, "Non pare diversa della *L. nivea* Vent."

1843—Lantana bartramii Baldwin, Reliq. Baldw. 247.

Type.—Not designated.

Taxonomic disposition.—L. × floridana? (see 1832)

Discussion.—The protologue cites no material. In a search of DWC, LASCA, MANCH, NY, P-DU, PH, WECO and WLU, only two historical specimens were located. At NY originally in the Torrey Herbarium (T. Zanoni, pers. comm.) is a specimen (!) labeled "grown in Louis Lecontes' Garden in Georgia" without collector or date and annotated as the "Lantana camara [var.] bartramii, cultivated in

Florida by Dr. Baldwin. This specimen may or may not have been seen by Baldwin. At PH, there is a sheet (dig. photo!) from the Muhlenberg Herbarium that has mounted on it several fragmentary specimens from different collectors. One such fragment is labeled, "1482 Lantana Hardy native" and presumably was collected by Baldwin. Further research is needed to determine if this specimen is original material. Both specimens are elements of *L. depressa* Small var. *floridana* (Moldenke) R.W. Sanders (see 1905).

Baldwin's protologue refers to plants along the Florida seacoast as being the same that Bartram described, without mentioning cultivated material. Bartram traveled only in the geographic range of var. *floridana*. Further, Baldwin describes the species as attaining the height of six feet. Material of *L. depressa* var. *floridana* that I have seen reaches three feet but not six. This, therefore, suggests Baldwin was describing the same hybrid that Rafinesque did under the name *Lantana* × *floridana*.

1844—Lantana hirsuta M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 11:326.

HOLOTYPE.—Mexico. Edo. Veracruz: Jalapa, Mirador, 1840, Gallioti 749 (BR [dig. photo!]; ISOTYPE: G [dig. photo!]).

Taxonomic disposition.—L. hirsuta (Setose Group)

1846—Camara vulgaris Benth., Bot. Voy. Sulphur 154.

LECTOTYPE (here designated).—Herb. Linnaeus 783.4 (LINN!).

Taxonomic disposition.—L. camara (see 1753)

Discussion.—This was a replacement name for Lantana camara when placed in Camara Adans. However, the correct name in Camara. is C. aculeata (L.) Kuntze (Rev. Gen. Plant. 2:503. 1891.)

1847—Lantana armata Schauer, Linnaea 20:480.

LECTOTYPE (here designated, cited as "isotype" by López-Palacios 1977).—Venezuela. "ad Caracas," Moritz 292 (BM, n.v.; HOLOTYPE now destroyed: B [Macbride Neg. 17463 F!, GH!]).

Name misapplied to:

L. camara (Moldenke 1972a)

Taxonomic disposition.—L. hirsuta (see 1844)

1847—Lantana polyacantha Schauer in DC., Prodr. 11:597.

HOLOTYPE.—Mexico, Schiede s.n. (B, destroyed, Macbride Neg. 17481 [F!]).

Taxonomic disposition.—L. horrida (see 1817)

1847—Lantana cujabensis Schauer in DC., Prodr. 11:599.

LECTOTYPE (Santos Silva 2001).—Brazil.Matto Grosso, *Manso s.n.*, Mart.Fl.Bras. 1026 (M, n.v.; ISOLECTOTYPES: BM, BR (2) [dig. photos!], G-DC [dig. photo!, Macbride Neg. 7873 F!, BRIT!], G [dig. photo!, Macbride Neg. 24632 F!, BRIT!], K, NY!).

Name misapplied to:

L. nivea (Moldenke 1981a)

L. viscosa (Moldenke 1984)

Taxonomic disposition.—L. cujabensis (Strigose Group)

Discussion.—The are two paratypes known to me. One is *Poeppig 1485* (Peru) at G. It apparently is annotated by Schauer (without his "!"). He cited *Poeppig 1405* which is probably a typographical error for "1485." The other is *Martius s.n.* (Brazil. Rio Negro) at M (n.v.).

1847—Lantana robusta Schauer in DC., Prodr. 11:601.

LECTOTYPE (Santos Silva 2001).—Brazil. Rio de Janeiro: "ad Padre do Correia," 1821, Pohl 40-5955 (W, n.v.). Taxonomic disposition.—L. robusta (Setose group)

Discussion.—There is a Macbride photograph (Neg. 17485 [F!, BRIT!, GH!, LL!, NY!]) of *Pohl 182* at B, now destroyed, that has been distributed as a photograph of a type. The specimen in the photograph should be disregarded as original material. This specimen neither appears to be annotated by Schauer nor bears sufficient inflorescence material to match the protologue. Furthermore, the paratype, *Raben 509* (NY [fragment]! and BR [photo at LL!]), and *Pohl 182* are not the same species.

Pohl 182 may belong to L. horrida or L. horrida X L. robusta.

1847—Lantana riedeliana Schauer in DC., Prodr. 11:601.

HOLOTYPE.—Brazil, Riedel s.n. (LE, n.v.).

Name misapplied to:

L. sp. sect. Callioreas (Moldenke 1970b)

Taxonomic disposition.—L. riedeliana or L. robusta?

Discussion.—The only original material cited is a unicate at LE, which did not respond to inquiries. There is a photograph in LL (perhaps by Moldenke) of Glazier 1651 that is annotated as L. riedeliana by Moldenke, as well as someone other than Schauer. This specimen appears to fit the description of L. riedeliana and suggests that L. riedeliana is conspecific with L. robusta, being a glabrescent, more narrow-leaved variant.

1847—Lantana pohliana Schauer in DC., Prodr. 11:601.

Type (Lectotype not designated).—Brazil, *Pohl s.n.* (W?, n.v.; duplicate: B, destroyed [Macbride Neg. 17480 F!, BRIT!, GH!]).

Taxonomic disposition.—L. pohliana or L. viscosa? (Setose Group?)

Discussion.—Schauer cited no collection number or herbarium. Pohl material should be at W, but no response to inquires there was received. Further investigation is needed.

1847—Lantana viscosa Pohl ex Schauer in DC., Prodr. 11:601.

LECTOTYPE (Santos Silva 2001).—Brazil. Goiás: "Ad Conceição, prope Trahiras," *Pohl 1876 & 2680* "D. nº 181." (left-hand specimen) (W, n.v.; ISOLECTOTYPE: B, destroyed [Macbride Neg. 17492 F!, BRIT!]) *Taxonomic disposition.—L. viscosa* (Setose Group)

1847—Lantana multicolor Lem., Fl. Serres Jard. Eur. 3:239.

Type.—Unknown.

Name misapplied to:

L. camara subsp. aculeata or its hybrid (Koch & Fintelmann 1858)

Taxonomic disposition.—L. camara subsp. aculeata, L. X mista, or L. sp. sect. Callioreas?

Discussion.—Seeds of this were sent to Brussels from Mexico, possibly of cultivated origin. Lemaire distinguished it from other cultivated lantanas by its unusually large leaves and by the rose and crimson flowering heads. Although Koch & Fintelmann (1858) recognized the species, they indicated that it may be a form of *L. camara* or *L. × mista*. However, the protologue also describes the heads as involucrate with four large bracts and with the floral bracts cordate-rotund. These characters would place the plants in section *Callioreas*.

1857—Lantana hybrida Neubert, Deutsch. Mag. Garten-Blumenk. 10:98. *nom. illeg. (nom. subnud.)* Lectotype (here designated).—icon in Neubert, Deutsch. Gart. Mag. 10:t. facing p. 112. Name misapplied to:

L. camara subsp. aculeata or L. strigocamara (Everett 1980)

Taxonomic disposition.—L. × flava (see 1775) or L. × mista (see 1767)

Discussion.—No specimens were found at HOH or STU to serve as lectotype or epitype. The description is very brief, indicating only the color of the flower heads. The plate shows nothing distinctive except for spreading hairs on the twigs, petioles, and peduncles, suggesting that the plants may be elements of L. \times flava or L. \times mista.

1858—Lantana formosa K. Koch & Fintelmann, Wochenschr. Gärtnerei Pflanzenk. 1:322. *nom. illeg., pro syn. sub L. crocea*

Type.—Unknown.

Taxonomic disposition.—L. camara (see 1753)

1863—Lantana triplinervia Turcz., Bull. Soc. Imp. Naturalistes Moscou 36:205.

HOLOTYPE.—Java, Goering 225 (KW?, n.v.).

Name misapplied to:

L. nivea (Moldenke 1974, 1977)

L. nivea × L. spp. Pilose Group (Moldenke 1974, in sched.; Sanders in sched.)

Taxonomic disposition.—L. nivea (see 1804)

Discussion.—Turczaninow described material that was cultivated or escaped from cultivation. The protologue strongly suggests *L. nivea* by the leaves long petiolate, ovate-lanceolate, triplinerved, apically acuminate, and minutely scabrous on the veins below.

1863—Lantana bahiensis Turcz., Bull. Soc. Imp. Naturalistes Moscou 36:206.

HOLOTYPE.—Brazil. Bahia, Salzmann s.n. (KW?, n.v.).

Name misapplied to:

L. nivea × L. spp. Setose Group (Moldenke in sched.)

Taxonomic disposition.—L. sp. sect. Callioreas

Discussion.—The protologue classifies this species in section Callioreas, which is corroborated by the description of bracts ovate, briefly acuminate, and 5-nerved.

1904—Lantana micrantha Briq., Annuaire Conserv. Jard. Bot. Gèneve 7-8:299.

HOLOTYPE.—Paraguay. Asunción, Balansa 1039 (G).

Name misapplied to:

L. horrida (Moldenke 1948, 1975d)

L. sp. sect. Callioreas (Moldenke 1981c)

Taxonomic disposition.—L. micrantha (Pilose Group)

1905—Lantana depressa Small, Bull. New York Bot. Gard. 3:436.

HOLOTYPE.—USA. Florida: Dade Co.: pinelands between Coconut Grove and Cutler, Small & Carter 747 (NY; ISOTYPE: F!).

Taxonomic disposition.—L. depressa (Strigose Group)

Discussion.—See Sanders (1987a)

1905—Lantana bahamensis Britton, Bull. New York Bot. Gard. 3:450.

Holotype.—Bahamas. New Providence: Ft. Montague, Britton & Brace 174 (NY!; Isotypes: F!, US!). Name misapplied to:

L. camara (Moldenke 1975a; Correll & Correll 1982 (pro parte))

L. depressa (Moldenke 1975c)

L. depressa × L. strigocamara Callowiana Hybrids (Moldenke, 1975b)

L. splendens (Moldenke in sched.; Correll & Correll 1982 (pro parte); Sanders in sched.)

Taxonomic disposition.—L. bahamensis (sp. hybrid origin between L. splendens and L. camara) Discussion.—Apparently Lantana camara, occurring in the southern Bahamas, began to hybridize introgressively into L. splendens, centered in the central Bahamas, shortly after settlement by Europeans. As a result, the native plants in the Bahamas are variable. The type of L. bahamensis shows the nitid surface and scattered geniculate hairs on the leaf undersurface venation typical of L. splendens, as well as the soft, erect hairs persisting along the undersurface veins, apparently expressing genes of L. camara. The bracts vary from oblong-lanceolate as in L. splendens to obovate-elliptic as in L. camara.

1905—Lantana ovatifolia Britton, Bull. New York Bot. Gard. 4:123.

Holotype.—Bahamas. Grand Bahama: Eight Mile Rocks, Britton & Millspaugh 2450 (NY!; ISOTYPE: F!). Name misapplied to:

L. depressa (Long 1970; Long & Lakela 1971; Moldenke 1982)

L. strigocamara × L. depressa (Long & Lakela 1971) = L. ×floridana Raf.

Taxonomic disposition.—L. ovatifolia (Strigose Group)

Discussion.—See Sanders 1987a.

1906—Lantana glandulosissima Hayek, Repert. Spec. Nov. Regni Veg. 2:161.

HOLOTYPE.—Mexico. Jalisco: Tequila, Pringle 4431 (W, n.v.; ISOTYPES: BR, F!, MO!, NY!).

Name misapplied to:

L. horrida (Méndez 2002)

Taxonomic disposition.—L. camara (see 1753)

1906—Lantana cummingiana Hayek, Repert. Spec. Nov. Regni Veg. 2:161.

HOLOTYPE.—Chile. Cumming 1065 (W, n.v.)

Taxonomic disposition.—L. horrida (see 1817) or L. hirsuta (see 1844)

1906—Lantana urticoides Hayek, Repert. Spec. Nov. Regni Veg. 2:162.

Type.—Not selected, to be lectotypified in a subsequent paper. (Syntypes: USA: Texas. Lindheimer Exsic. No. 503, which includes two different Lindheimer numbered collections, F!, GH!, MO!, UC!, W, n.v.; Texas: Comal Co. *Matthes 19*, W, n.v.).

Name misapplied to:

L. horrida (Moldenke 1981b)

Taxonomic disposition.—L. urticoides (Setose Group)

Discussion.—See L. rubra 1832 above.

1907—Lantana foetida Rusby, Bull. New York Bot. Gard. 4:431.

HOLOTYPE.—Bolivia, Bang 2034=469 (NY [n.v., dig. photo not available]; ISOTYPES: US!, GH!).

Taxonomic disposition.—L. horrida (see 1817)

1909—Lantana weberbaueri Hayek in Urb., Bot. Jahrb. Syst. 42:166.

HOLOTYPE.—Peru. Junin: Tarma: Palca, Weberbauer 2017 (GB?, n.v., W?, n.v., or B? [destroyed, Macbride Neg. 17493, LL!]).

Taxonomic disposition.—L. weberbaueri or L. viscosa (see 1847) or its hybrid? (Setose group)

Discussion.—This is a rare, poorly known species. Hayek's opinion was that it is near *L. viscosa* and *L. robusta* in the Setose Group of section *Lantana*.

1910—Lantana arida Britton, Bull. Torrey Bot. Club 37:357.

HOLOTYPE.—Jamaica, Fort Henderson, Britton & Hollick 1824 (NY!).

Name misapplied to:

L. camara (Moldenke, 1982a)

L. horrida (Moldenke, 1982a; Méndez, 2002)

Taxonomic disposition.—L. horrida (see 1817)

Discussion.—This is a small-leaved variant of Antillean L. horrida, perhaps as a growth response to drought conditions.

1912—Lantana subcordata Urb., Symb. Antill. 7:351.

LECTOTYPE (here designated).—Dominican Rep. near Santiago, Schomburgh 5 (K! [HOLOTYPE: B, destroyed]; ISOLECTOTYPE: P).

Taxonomic disposition.—L. subcordata (Pilose Group)

Discussion.—See Sanders 1989a

1922—Lantana pulchra Larrañaga, Escritos D. A. Larrañaga 1:406. nom. dub.

Type.—Destroyed.

Taxonomic disposition.—Cannot be determined.

Discussion.—Written in the style of the Linnaeans, the protologue contains only 14 words besides the binominal and provides no features to distinguish it from other published species. As both the specimens and Larrañaga's drawings are destroyed (E. A. Paz, MVFQ, pers. comm.), the name must be treated as a *nomen dubium*.

1934—Lantana tenuifolia Rusby, Phytologia 1:74.

HOLOTYPE.—Bolivia. Bopi River, Rusby 653 (NY [n.v., dig. photo not available]).

Taxonomic disposition.—L. cujabensis? (see 1847)

1940—Lantana insularis Moldenke, Caribbean Forester 2:16.

HOLOTYPE.—Jamaica. trail from St. Helens Gap to Latimer River, Maxon & Killip 912 (NY!; ISOTYPE: US!). Taxonomic disposition.—L. insularis (Setose Group)

1940—Lantana leonardiorum Moldenke, Caribbean Forester 2:17. Published as *L. "leonardorum"* Holotype.—Haiti. near Jean Rabel, *Leonard & Leonard 13782* (NY!; ISOTYPES: A!, GH!, US!).

Taxonomic disposition.—L. leonardiorum (Pilose Group)

Discussion.—See Sanders 1989a

1940—Lantana scorta Moldenke, Publ. Carnegie Inst. Washington 522:161.

HOLOTYPE.—Mexico. Queretaro: near San Juan de Río, Rose et al. 9520 (NY!).

Name misapplied to:

L. horrida (Moldenke in sched.)

L. camara× L. horrida× L. hirsuta (Moldenke 1940)

Taxonomic disposition.—L. hirsuta (see 1844)

1940—Lantana notha Moldenke, Phytologia 1:422.

HOLOTYPE.—Mexico. Sinaloa: Fuerte, Rose et al. 13573 (NY!).

Taxonomic disposition.—L. notha? (section?)

Discussion.—Although Moldenke (in sched.) applied this name to plants in section Lantana, the type appears to be in section Callioreas, but the critical character to distinguish sections, mature fruits, is lacking.

1941—Lantana scandens Moldenke, Phytologia 2:18.

Holotype.—Mexico. Michoacán: Coalcomán: Villa Victoria, Pto. de Aire, Hinton 12315 (NY!; ISOTYPES: F!, LL!, MO!, NY!, US!).

Taxonomic disposition.—L. scandens or L. scabrida (see 1789 Strigose Group)

1941—Lantana brittonii Moldenke, Phytologia 2:52.

Holotype.—Jamaica. Tweedside, below Moody's Gap, Harris & Britton 10541 (NY!; ISOTYPE: US!). Taxonomic disposition.—L. scabrida (see 1789)

1946—Lantana minasensis Moldenke, Phytologia 2:138.

Holotype.—Brazil. Minas Geraes: KM 2 along road from Viçosa to Barroso, *Mexia 4448a* (NY [dig.photo!]; Isotypes: MO!, TEX!).

Name misapplied to:

L. nivea (Moldenke 1946)

L. nivea × L. spp. Pilose Group (Moldenke 1966, 1972a, 1973a, in sched.; Sanders in sched.) Taxonomic disposition.—L. nivea (see 1804)

1962—Lantana kingii Moldenke, Phytologia 8:161.

HOLOTYPE.—Mexico. Oaxaca: 2 km south of Niltepec, King 1775 (TEX!; ISOTYPE: US!) Taxonomic disposition.—L. kingii or L. scabrida (see 1789, Strigose Group)

1979—Lantana morii Moldenke, Phytologia 41:449.

Holotype.—Brazil. Bahia: Mun. Camacã: São João do Panelinha, Santos & Mattos 3304 (LL!; ISOTYPE: NY!). Taxonomic disposition.—L. nivea (see 1804)

1987—Lantana hodgei R.W. Sanders, J. Arnold Arbor. 68:343.

Holotype.—Dominica. Fresh Water Lake, elfin forest, Fosberg 48269 (US!; ISOTYPES: F!, GH!, K, MO!, NY!). Taxonomic disposition.—L. hodgei (Strigose Group)

2006—Lantana strigocamara R.W. Sanders, in this publication.

HOLOTYPE.—USA. Florida: Dade Co., Sanders 1450 (FTG!; ISOTYPE: NY!). (Fig. 4)

Taxonomic disposition.—L. strigocamara (L. spp. Strigose and Setose Groups \times L. camara subsp. aculeata)

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